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LYDELLA NIGRIPES AND L. PINIARIAE, FLY PARASITES OF CERTAIN TREE-DEFOLIATING CATERPILLARS [1]

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INTRODUCTION

For a number of years the United States Bureau of Entomology has been collecting the European parasites of the gipsy moth (*Porthetria dispar* L.) and the brown-tail moth (*Nygmia phaeorrhoea* Don.) for liberation in New England. The tachinid fly *Lydella nigripes* Fallén is a minor parasite of both these pests. Its mode of life is similar to that of *Compsilura concinnata* Meig., which became established in the United States in 1907. *C. concinnata* has proved highly successful in its new environment, and it was believed that *L. nigripes* might do as well if once established. Accordingly, in 1928 and 1929, a special attempt was made to secure large numbers of the species from Europe. At that time it was noted from the literature that the species overwintered as a first-instar larva in the pupa of the pine geometrid (*Bupalus piniarius* L.). A heavy outbreak of *B. piniarius* in northwestern Poland at Chorinskimlyn seemed to present an excellent opportunity to rear the parasite, and 100,000 host pupae were collected in the spring of 1928. Recoveries were disappointingly small. Only about 1,800 puparia were secured. These were all sent to the laboratory of the Bureau of Entomology at Melrose Highlands, Mass., for colonization. In 1929 the work was continued on a larger scale at Zwierzyniec, near Lwow, Poland, and about 57,000 puparia were obtained.

The same year biological investigations of the species were started. The flies reared from *Bupalus piniarius* behaved in a manner very different from what had been expected. They practically refused to attack either gipsy or brown-tail moth larvae, in spite of the fact that specialists in Tachinidae considered flies reared from the three hosts to be identical. Investigations of that year and subsequent ones have shown that flies reared from *B. piniarius* actually have very different habits and life histories from those of flies reared from *Porthetria dispar* or *Nygmia phaeorrhoea*. It was possible, though, to show that flies reared from *P. dispar* and *N. phaeorrhoea* were identical. Those

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reared from *P. dispar* and *N. phaeorrhoea* are the true *Lydella nigripes* Fallén, while those from *B. piniarius* are *Lydella piniariae* Hartig.

This paper presents a study of the bionomics of these two species of Lydella and a comparison of their life histories, and shows their close relationship. The true *L. nigripes* has been studied in particular because of its importance as a parasite of the gipsy and brown-tail moths. This species has also been compared briefly with *Compsilura concinnata*.

REVIEW OF LITERATURE

Although a full account of the biology of *Lydella nigripes* has never been published, references to the species are common in the literature. These references do not distinguish between *L. nigripes* (*Dexodes nigripes*) and *L. piniariae*, but when they give *Porthetria dispar*, *Nygmia phaeorrhoea*, or *Bupalus piniarius* as the host species parasitized, there is little question as to the identity of the parasite.

LYDELLA NIGRIPES

In 1908 Townsend (*17*) [3] noted briefly the manner in which *Lydella nigripes* deposited living maggots beneath the skin of host caterpillars and its rapid development in larvae of *Euproctis chrysorrhoea* L. (=*Nygmia phaeorrhoea*) and *Heterocampa leucostigma* S. and A. Pantel (*10*) in 1910 stated that it belonged to the same group as *Compsilura concinnata*, which he described in some detail. Howard and Fiske in 1911 (*7*) and Burgess and Crossman in 1929 (*3*) briefly noted the life history of the species. They also gave summaries of the number of *L. nigripes* puparia recovered from rearings of European *Nygmia phaeorrhoea* and *Porthetria dispar*, and the number of flies liberated in the United States, with a discussion of the possiblity of the species becoming established in North America.

LYDELLA PINIARIAE

In 1914 Plotnikov (*11*), in a paper on the biology of *Bupalus piniarius* and its parasites, considered *Lydella nigripes* (=*piniariae*) one of the most important parasites of that species. He described its life history in this host briefly, figuring and describing the first larval instar in detail. In 1921 Baer (*1*) called attention to the polyphagous habits of the species, and emphasized its importance as a parasite of *B. piniarius*. Seitner (*12*) mentioned it in 1921, and Sitowski (*13*) in 1922, Eidmann (*5*) in 1926, Czerwinski and Kuntze (*4*) in 1930, and Steiner (*14*) in 1931 briefly sketched its life history and gave valuable information regarding its effectiveness as a parasite of *B. piniarius*. In 1931 Escherich (*6, v. 3, p. 463–569*) reviewed these references in a comprehensive study of *B. piniarius*.

DISTRIBUTION AND HOST RELATIONSHIPS

Lydella nigripes is common throughout Europe. Rearings of gipsy and brown-tail moth material in connection with the work of the United States Bureau of Entomology show recoveries from Spain, France, Italy, Belgium, Holland, Germany, Czechoslovakia, Switzerland, Austria, Hungary, Yugoslavia, Poland, and Russia. Probably its range is even greater.

[3] Reference is made by number (italic) to Literature Cited, p. 994.

Lydella piniariae is also common throughout Europe, if we may judge from the fact that *L. nigripes* is recorded as a parasite of *Bupalus piniarius* in France, Germany, Austria, Czechoslovakia, Denmark, Poland, and Russia.

A remarkably large number of hosts for *Lydella nigripes* are mentioned in European literature. Since no distinction is made between *L. nigripes* and *L. piniariae*, the references may, of course, refer to either one. The writer's experiments showed, however, that *L. nigripes* was exceptionally polyphagous, whereas *L. piniariae*, although given almost as many host larvae to attack, was able to complete development only in *Bupalus piniarius*, *Abrostola tripartita* Hufn., and *Tortrix dumetana* Freyer. It has therefore seemed advisable to make two host lists. The first gives records from the literature. The second gives records which were made in connection with this study from larvae parasitized in the laboratory and from collected larvae that had been parasitized under natural conditions in the field.

HOSTS OF LYDELLA NIGRIPES AS RECORDED IN THE LITERATURE

Lepidoptera:
- *Acronicta rumicis* L. (*1*).
- *Agrotis candelarum* Stdgr. (*2*).
- *Aporia crataegi* L. (*8*).
- *Acosmetia caliginosa* Hbn. (*2*).
- *Bupalus piniarius* L. (*2*).
- *Brephos parthenias* L. (*9*).
- *Calymnia trapezina* L. (*9*).
- *Cucullia artemisiae* Hufn. (*9*).
- *Cucullia asteris* Schiff. (*2*)
- *Cucullia scrophulariae* Cap. (*9*).
- *Deilephila euphorbiae* L. (*2*).
- *Dendrolimus pini* L. (*1*).
- *Dryobota protea* Bkh. (*9*).
- *Euproctis chrysorrhoea* L. (*1*).
- *Eurrhypara urticata* L. (*2*).
- *Heliothis scutosa* Schiff. (*2*).
- *Hematurga atomaria* L. (*5*).
- *Hybernia* sp. (*2*).
- *Larentia badiata* Hbn. (*1*).
- *Leucania pallens* L. (*1*).

Lepidoptera—Continued
- *Lymantria dispar* L. (*1*).
- *Mamestra pisi* L. (*2*).
- *Miana literosa* Haworth (*2*).
- *Ortholitha cervinata* Schiff. (*2*).
- *Phragmatobia fuliginosa* L. (*2*).
- *Plusia gamma* L. (*2*).
- *Polia oleracea* L. (*19*).
- *Porthesia similis* Fuess. (*2*).
- *Tapinostola elymi* Treit. (*2*).
- *Tephroclystia innotata* Hufn. (*9*).
- *Tephroclystia virgaureata* Dbl. (*2*).
- *Thaumetopea pinivora* Treit. (*2*).
- *Vanessa io* L. (*2*).
- *Vanessa polychloros* L. (*2*).
- *Vanessa urticae* L. (*2*).
- *Yponomeuta padellus* L. (*1*).

Hymenoptera:
- *Lophyrus* sp. (*2*).
- *Nematus ribesii* Scopoli (*2*).

HOSTS OF LYDELLA NIGRIPES DETERMINED FROM REARINGS IN EUROPE

LARVAE PARASITIZED UNDER NATURAL CONDITIONS IN THE FIELD

Lepidoptera:
- *Abrostola tripartita* Hufn.
- *Arctia caia* L.
- *Malacosoma neustria* L.
- *Nygmia phaeorrhoea Don.*
- *Porthesia similis* Fuess.

Lepidoptera—Continued
- *Porthetria dispar* L.
- *Polia trifolii* Rott.
- *Thaumetopoea processionea* L.
- *Vanessa urticae* L.

LARVAE PARASITIZED IN THE LABORATORY

Lepidoptera:
- *Abrostola triplasia* L.
- *Acronicta megacephala* Fab.
- *Acronicta rumicis* L.
- *Acronicta tridens* Schiff.
- *Agrotis c-nigrum* L.
- *Calophasia casta* Bkh.
- *Cucullia asteris* Schiff.
- *Eriogaster lanestris* L.
- *Heliothis dipsacea* L.

Lepidoptera—Continued
- *Oxycesta geographica* Fab.
- *Phalera bucephala* L.
- *Polia brassicae* L.
- *Polia oleracea* L.
- *Synopsia sociaria* Hbn.
- *Vanessa io* L.

Hymenoptera:
- *Trichiocampus viminalis* (Fall.).

Lydella nigripes also completed development on two lepidopterous larvae attacked at the gipsy moth laboratory at Melrose Highlands, Mass., namely, *Alypia octomaculata* Fab. and *Heterocampa leucostigma* S. and A.

Under natural conditions in the field *Lydella piniariae* parasitized larvae of *Bupalus piniarius* L. (Lepidoptera) and in the laboratory it parasitized larvae of *Tortrix dumetana* Freyer and *Abrostola tripartita* Hufn. (both Lepidoptera).

With the two exceptions noted all attempts to rear *Lydella piniariae* at the laboratory were unsuccessful. Judging from the long list of successful laboratory rearings of *L. nigripes*, one feels that the great majority of hosts given in the literature actually belong to this species.

ECONOMIC IMPORTANCE

LYDELLA NIGRIPES

The early work on *Lydella nigripes* done at the Melrose Highlands laboratory indicated that this insect was important as a parasite of the brown-tail moth in Europe. It was reared in small numbers from shipments of larvae in 1906, 1907, and 1911, and in fairly satisfactory numbers in 1909. A total of 5,212 was secured during this period. At that time it was rarely reared as a parasite of the gipsy moth.

Since the foreign work was resumed in 1922 no large collections of *Nygmia phaeorrhoea* have been made, but *Lydella nigripes* has at times been of some importance as a parasite of *Porthetria dispar*. Table 1 gives the number of puparia recovered.

TABLE 1.—*Recovery of Lydella nigripes and total tachinid puparia from collections of Porthetria dispar in Europe, 1926 to 1931, inclusive*

Year	Place of collection	*P. dispar* larvae collected	*L. nigripes* puparia recovered	Total tachinid puparia recovered
1926	Galgamacsa, Hungary	225,000	2,784	58,398
	Baja, Hungary	300,000	870	80,451
1927	Doboz, Hungary	250,000	1,023	11,965
	Olaszliszka, Hungary	400,000	1,847	40,971
	Simontornya, Hungary	188,000	1,734	35,537
	Rembertow, Poland	200,000	183	51,566
	Moscenica, Yugoslavia	150,000	293	11,388
1928	Vecs, Hungary	230,000	77	42,734
	Novoselec Kriz, Yugoslavia	178,000	25	44,756
1929	Vecs, Hungary	189,000	0	14,224
	Platicevo, Yugoslavia	239,000	0	14,415
1930	Jánk, Hungary	320,000	10	37,289
	Oszro, Hungary	238,000	5	95,819
	Csepel, Hungary	4,000	0	641
	Platicevo, Yugoslavia	250,000	0	28,374
1931	Galgamacsa, Hungary	331,000	10	11,514
	Oszro, Hungary	406,000	540	93,199
	Oberpullendorf, Austria	230,000	31	73,108

In 1927, 1930, and 1931 a few *Nygmia phaeorrhoea* larvae were collected. A record of the *Lydella nigripes* reared is given in Table 2.

TABLE 2.—*Lydella nigripes puparia reared from collections of Nygmia phaeorrhoea in Europe, 1927, 1930, and 1931*

Year	Place of collection	*N. phaeorrhoea* larvae collected	*L. nigripes* puparia reared
1927	Budapest, Hungary	250	44
	do	1,565	10
1930	Jánk, Hungary	126	55
	Oszro, Hungary	83	0
	Platicevo, Yugoslavia	300	0
	Linz, Austria	1,200	18
1931	Budapest, Hungary	1,500	16
	Oberpullendorf, Austria	1,000	48

LYDELLA PINIARIAE

Lydella piniariae is much more important in controlling *Bupalus piniarius* than is *L. nigripes* in controlling the gipsy moth and the brown-tail moth. It is generally present in comparatively small numbers in the first year of a Bupalus infestation, but after that it increases rapidly. Plotnikov (*11*) notes it as parasitizing 12 per cent of the larvae and Sitowski (*13*) records it as parasitizing 25 per cent. The writer's rearings are recorded in Table 3.

TABLE 3.—*Recovery of Lydella piniariae puparia from collections of Bupalus piniarius in Europe, 1928, 1929, and 1930*

Year	Place of collection	Overwintering *B. piniarius* pupae collected	*L. piniariae* puparia recovered	Parasitization by *L. piniariae*
		Number	*Number*	*Per cent*
1928	Chorinskimlyn, Poland	120,000	1,836	1.5
1929	Zwierzyniec, Poland	735,000	57,838	7.8
1930	Gora, Poland	3,000	600	20.0

DESCRIPTION

The adult flies of *Lydella nigripes* and *L. piniariae* have been separated by W. F. Sellers, of the gipsy moth laboratory. Papers by Thompson (*15*) and by Thompson and Thompson (*16*) have been very helpful in preparing the descriptions of the immature forms.

ADULT

A description of *Lydella nigripes* (fig. 1) by Lundbeck (*9, pt. 7, p. 299*) in its main essentials is an excellent description of the two forms treated in this paper, but it does not serve to differentiate them. According to Sellers, however, the two species can be readily distinguished by the relationship of the front at its narrowest point to the head at its widest part. The ratio was secured by dividing the smaller measurement by the larger. *L. nigripes* has an average range of from 0.224 to 0.245 mm in the males, and from 0.293 to 0.308 mm in the females, while *L. piniariae* has an average range of from 0.274

to 0.286 mm in the males, and from 0.324 to 0.333 mm in the females. Since the two forms are readily separated and do not show a natural tendency to interbreed, it is believed that they have become sufficiently stabilized to be considered as having a more specific than racial relationship.

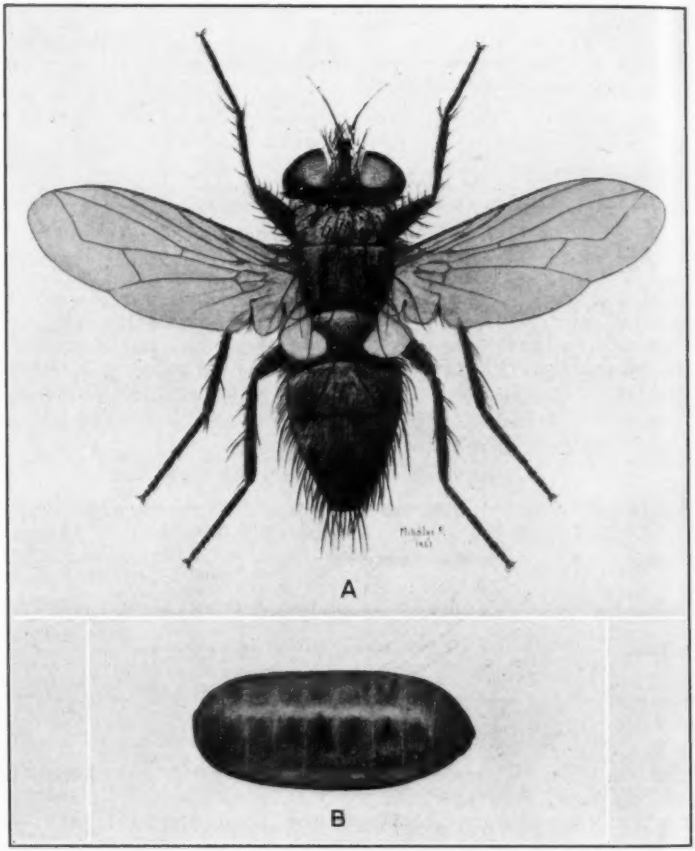

FIGURE 1.—*Lydella nigripes:* A, Adult female; B, puparium

Sellers found that both forms were included in the type series of both species. He concludes that the bulk of the synonymy probably represents the form reared from *Porthetria dispar* and numerous other hosts—i. e., the one with the smallest ratio—and that this is the true *Lydella nigripes* Fallén, while the form reared from *Bupalus piniarius* is *L. piniariae* Hartig. In Meigen's collection at Vienna, Austria, there are two cotypes of *nigripes* Fallén. Sellers has designated the male as the true *nigripes;* the female is *Lydella piniariae* Hartig.

IMMATURE STAGES

LYDELLA NIGRIPES

THE EGG

When the egg enters the uterus it measures about 0.66 mm long and 0.21 mm wide. It has the form of an ellipse, but is rounded off at each end. The chorion is very thin and transparent over the entire surface except in the terminal micropyle region, where it is somewhat thicker and roughened. With the development of the embryo to a fully formed larva, the chorion stretches considerably.

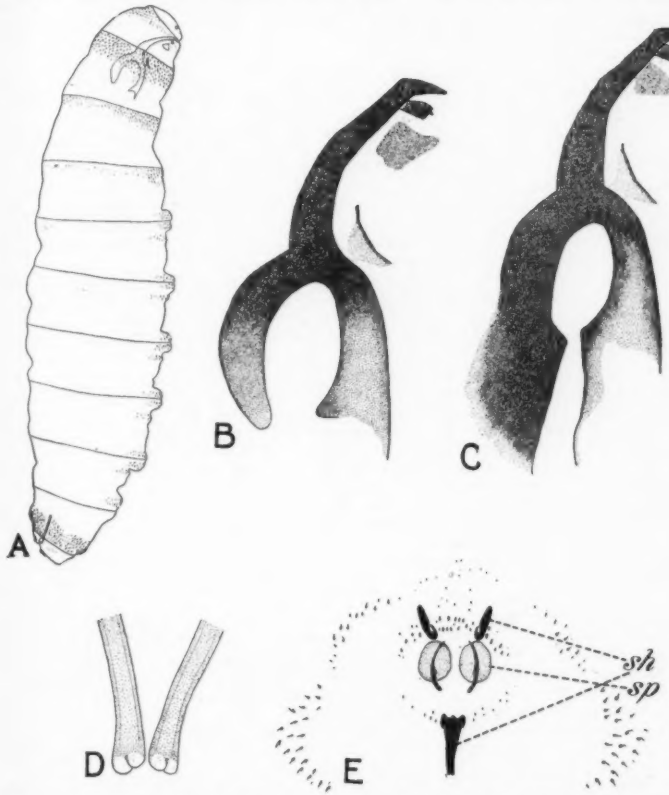

FIGURE 2.—*Lydella nigripes*, first larval instar: A, larva, lateral aspect; B, buccopharyngeal armature of freshly larviposited specimen; C, buccopharyngeal armature of 4-day-old specimen; D, posterior spiracle chambers; E, posterior spiracles, *sp*, showing cuticular armature of eleventh segment, and stigmatic hooks, *sh*

FIRST-INSTAR LARVA

The first-instar larva of *Lydella nigripes* (fig. 2, A) is cylindrical, tapering slightly at both extremities. Freshly deposited specimens are from 0.90 to 1.20 mm long and from 0.30 to 0.35 mm wide. Full-grown first-instar larvae average 2 mm in length and 0.75 mm in width. The body is composed of the pseudocephalon, bearing the antennal and sensorial organs, and 11 body segments. The cuticle is colorless and transparent, so that the tracheae and portions of the diges-

tive system are plainly visible. The pseudocephalon is unarmed, but on every other segment the cuticle bears rows of minute spines. The first three anterior (thoracic) segments are completely encircled anteriorly. The fourth (first abdominal) segment has a complete anterior band of spines, which are quite scattered in the pleural region. Ventrally this band is divided into two groups which are separated longitudinally by a narrow but well-defined bare space. This segment also bears a small group of spines ventrally on its posterior border. On segment 5 the encircling anterior band is absent. There are a few very small dorsal spines, but none in the pleural region. Ventrally there are two narrowly separated groups on the anterior border and a small group on the posterior border as on segment 4. The arrangement of spines on segments 6 to 9 is practically identical with that on segment 5 except that the few dorsal spines are lacking. Segment 10 bears no anterior spines, but it has a completely encircling band on its posterior border. The eleventh segment has no bands of spines comparable to those of the other segments, but it supports the three curious and interesting stigmatic hooks (fig. 2, E) which are characteristic of this type of larva. Two of them lie just anterior to the anal spiracles, and are simple strongly curved hooks about 0.015 mm long. They are directed forward. The third, which measures 0.02 mm, occupies a position midway between the first two but posterior to the anal spiracles. At its anterior extremity it is divided into two hooks that point backward. These hooks are used in this species, as Pantel (*10*) described them in *Compsilura concinnata*, to attach the larva to the intestine of the host. Besides these hooks there are a few spines on the pleural portion of the eleventh segment and also surrounding the spiracular openings.

The arrangement of the cuticular spines in rows is indicated in Figure 2, A. Those on the anterior borders of the segments point backward, while those on the posterior borders point forward. The rows of spines have no absolutely definite arrangement, but for the most part each spine in one row occurs opposite the space between two spines in the row preceding it.

The fact that each segment from the fourth to the eighth, inclusive, has a row of ventral spines on the posterior border followed closely by two rows of spines on the anterior border of the following segment gives the larva the superficial appearance of having segments bearing three closely situated rows of spines ventrally. This appearance is so deceptive that Plotnikov (*11*) described the larva in this manner, but he did not study the later larval instars, which show the true relation more clearly. The reason the location of the actual segmental division is so hard to define is that the spines occur on the pseudopodia or false feet, which are formed by flesh growing internally between the segments on the venter, thus pushing the cuticle out.

The buccopharyngeal armature of the freshly emerged larva is shown in Figure 2, B. It is about 0.18 mm long. The median tooth is a single piece which is divided at the basal region into two pairs of basal wings. There are two pairs of lateral plates at the apex of the armature and a single salivary gland plate at the base of the median tooth. As the larva grows the form of the armature is considerably changed owing to the progressive sclerotization[4] which takes place in the pharyngeal cuticle surrounding the basal plates. (Fig. 2, C.)

The larva is metapneustic. The two posterior spiracles open on the dorsopleural portion of the last abdominal segment. The spiracular chambers (fig. 2, D) are about six times as long as wide and measure 0.06 mm in length. From these chambers a well-developed tracheal system arises in two main tracheal trunks, which lie dorsally in the body cavity.

The only sensory organs observed in the larva are located on the pseudocephalon. There are four pairs, one element of each lying on opposite sides of the mouth opening. The most conspicuous are the antennal organs, which are circular, slightly protuberant, and measure 0.0075 mm in diameter. Just below them are the maxillary organs, composed of a group of about 10 minute circular points very slightly raised from the surface of the cuticle. Just below the antennae are two minute organs and just below each maxillary group another minute organ is found. The last two groups are so small that they are impossible to find in most specimens. A very delicate fold surrounds the antennal and maxillary organs, thus raising the group slightly from the rest of the cuticle.

[4] "Sclerotization" as used in this paper refers to the darkening and hardening of the area.

SECOND-INSTAR LARVA

As the first-instar larva approaches maximum growth the organs of the second instar can be plainly seen forming under the skin. The old skin finally splits just above the anal spiracles and larval movement forces it over the head. The second-instar larva (fig. 3, A) is considerably larger than the first-instar larva, measuring about 3 mm long and 1 mm wide when first formed and about 5.33 mm long and 1.75 mm wide when full grown. It has the same form as the first-instar larva and the cuticle is still colorless and transparent. The cuticular armature is heavier and more conspicuous. The rows are now formed of lineal groups of from 4 to 12 spines. These groups are quite distinctly separated from one another

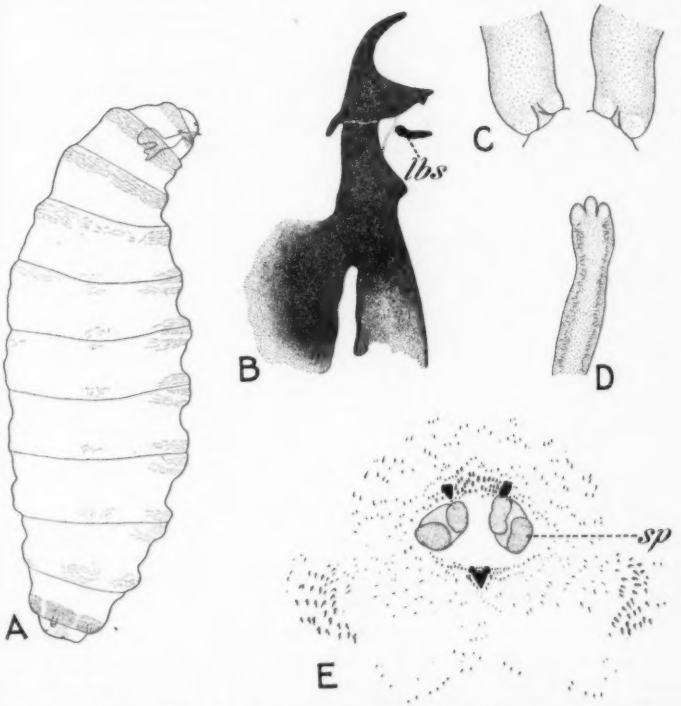

FIGURE 3.—*Lydella nigripes*, second larval instar: A, larva, lateral aspect; B, buccopharyngeal armature showing labial sclerite, *lbs;* C, posterior spiracle chambers; D, anterior spiracle chamber; E, posterior spiracles, *sp*, showing surrounding cuticular armature

and curved so that the rows become indistinct, but the arrangement is much the same as in the first instar. The pseudocephalon bears no spines. The first three segments have anterior bands of spines only. The fourth segment bears a completely encircling band of spines on its anterior border, but in the pleural region the spines are rather scattered. This segment bears spines on its posterior border also. On the fifth segment the anterior band is distinctly broken by a bare area on each side of the small pleural group. In the ventral region this band is made up of two groups of spines separated by a narrow longitudinal bare strip. Each of these areas has about four rows of spines, but the anterior one is nearly uniform in width while the posterior one is considerably longer and much narrower, or is even broken at the center. On the posterior border of this segment there is a small group of spines in the ventral region and also in the pleural region. Segments 6 to 9 are much the same as segment 5. On segment 6 the dorsal spines on the anterior border have practically disappeared, and the anterior pleural spines

are reduced. On segments 7, 8, and 9 the spines on the anterior borders are present only ventrally, where they diminish slightly in numbers proceeding posteriorly. The spines on the posterior borders, however, increase in numbers slightly on the seventh and eighth segments, and on the ninth segment the posterior pleural group is quite prominent and a few posterior dorsal spines are present. The tenth segment bears a complete band on its posterior border. In this band there is an almost bare area both dorsopleurally and ventropleurally. The eleventh segment bears no spines comparable to those of the other segments. The stigmatic hooks are situated as before, but in this instar each is an aggregate of hooks rather than a single piece. The anterior pair have two or three forward-pointing hooks, which are fused at their bases into a small, irregularly shaped area. The posterior element is made up of five or six hooks which point backward. The fusion of their bases forms a V-shaped sclerite. (Fig. 3, E.) On the sides of this segment there are a few rows of spines and scattered over the whole segment there are small spines.

The arrangement of the cuticular armature is shown in Figure 3. The direction of the spines is the same as in the first instar. The pseudopodia are more pronounced.

The buccopharyngeal armature (fig. 3, B) has undergone considerable change. Instead of a single median tooth, there is a pair of deeply curved anterior hooks which are separated from the basal region by a narrow incision. Lateral plates at the apex of the anterior hooks are no longer present. Just below the posterior margins of the hooks two small sclerites can be distinguished. These support the labium. When the structure is viewed in its ventral aspect, the labium can be distinguished between the bases of the anterior hooks, posterior to the labium the hypopharyngeal plate, and below that the epipharyngeal plate. Both of these plates are essentially the same in the third instar, and are described in more detail in the next section. There is no progressive sclerotization in the basal region of the second-instar buccopharyngeal armature. Immediately after the first-instar larval skin is shed only the anterior portions of the hooks are sclerotized, but sclerotization of the rest of the armature takes place very rapidly. Usually the edge of the dorsal wing is not fully pigmented.

The second-instar larva is amphipneustic. The anterior spiracles (fig. 3, D) open on the posterior border of segment 1 in the pleural region. Each has three respiratory papillae and a lightly colored forechamber leading to the tracheal tubes. The posterior spiracles (fig. 3, C) open on the dorsopleural portion of the eleventh segment. The spiracular chambers are about twice as long as wide. The tracheal system is much heavier than in the first instar.

The sensory organs on the pseudocephalon have about the same appearance as in the first instar, but they are larger and more conspicuous. In this instar there are also two pairs of sensory organs on the eleventh body segment. They are tiny fingerlike projections; each element of one pair is situated on each side of the posterior spiracular hook, and each element of the other pair is placed just inside one of the anterior spiracular hooks.

THIRD-INSTAR LARVA

The third-instar larva (fig. 4, A) has the same form as in the preceding instar. Its size varies greatly. When first formed it is about 6 mm long and 2 mm wide, when full grown from 7 to 9 mm long and from 2 to 2.50 mm wide. The cuticle is colorless and transparent and armed, as before, with tiny spines, but there is considerable variation in their pigmentation so that in some specimens they are more difficult to see than in others. The spines are again arranged in curved lineal groups, which are even more distinctly separated than in the second instar.

The pseudocephalon is unarmed. Segments 1 to 3 have anterior bands of spines only. On segment 4 the anterior band is interrupted in the pleural region, while ventrally it is widened into two groups slightly separated from each other by a narrow longitudinal bare area. On the posterior border of this segment there is a small ventral and a small pleural group of spines. On segment 5 the anterior band of spines is more distinctly broken in the pleural region, while ventrally the two groups are distinctly separated. The anterior of these groups is rather short but of an even width throughout. The posterior group is longer but very narrow or broken at the center. The posterior border of this segment is armed similarly to segment 4, but the pleural group is longer. Segments 6 to 9 are armed similarly to segment 5, but proceeding posteriorly the spines on the anterior borders of the segments become less numerous and those on the posterior borders more plentiful. On segment 9 the posterior border is completely encircled. On segment 10 the band on the posterior border is complete and heavy throughout, although there is

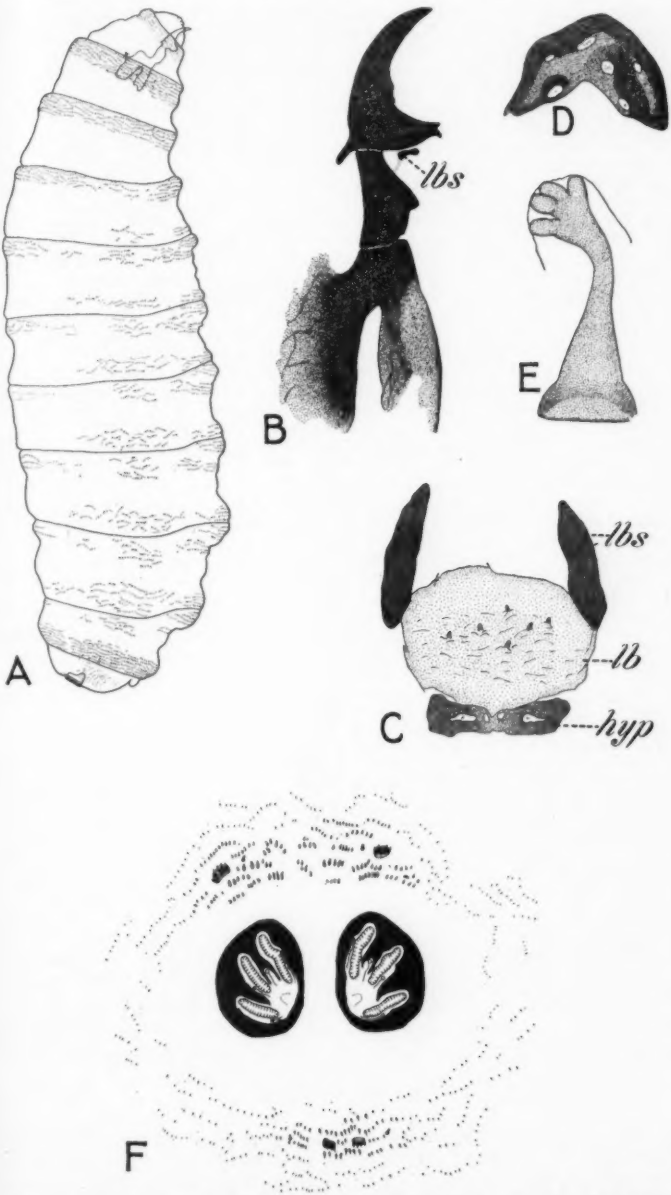

FIGURE 4.—*Lydella nigripes*, third larval instar: A, Larva, lateral aspect; B, buccopharyngeal armature, showing labial sclerite, *lbs;* C, hypopharyngeal plate, *hyp*, labial sclerite, *lbs*, and labium, *lb;* D, epipharyngeal plate; E, anterior spiracle chamber; F, posterior spiracles, showing surrounding cuticular armature

a narrow bare area in the dorsopleural region. Segment 11 bears the heavy posterior spiracles on its upper caudal aspect (fig. 4, F), which are surrounded by rather stout spines. The stigmatic hooks are lacking, but in the positions that they occupy in the earlier instars appear little clusters of three or four spines with their bases fused together to form a pigmented plate. Often there are two such groups posteriorly. Aside from the spines around the spiracles there is a conspicuous group of spines that are directed away from the spiracles.

The direction of the spines is again the same in this instar, and the pseudopodia are even more pronounced than in earlier instars.

The form of the buccopharyngeal armature (fig. 4, B) does not differ greatly from that observed in the preceding instar, but an articulation exists between the base of the intermediate region and the basal plates. The sclerites which support the labium are again apparent, just below the posterior margin of the anterior hooks. Figure 4, C, shows the inner surface of the labium with its supporting sclerites on each side, and just posterior to it is the hypopharyngeal plate. This plate varies considerably in different specimens. Sometimes the two openings on each side are fused together, and sometimes the two sides are separated by a suture at the middle, although the general form is that given in the figure. The epipharyngeal plate (fig. 4, D) is found just dorsad of the hypopharyngeal plate near the center of the space formed by the two sides of the intermediate wings of the buccopharyngeal armature. It is even more variable in structure than the hypopharyngeal plate. Sometimes it has a very sharp angle at the apex and often some of the openings are not visible. The figure is taken from a fairly representative specimen. Progressive sclerotization of the armature takes place as in the second instar.

In the third instar the larva is again amphipneustic. The anterior spiracles (fig. 4, E) have three or four papillae. The lightly sclerotized tube leading to the tracheae is narrowed behind the respiratory papillae, and then gradually widens out into a cup-shaped base. Each of the posterior spiracles (fig. 4, F) possesses three respiratory slits surrounded by a heavily pigmented horny area. The spiracular chambers are short and somewhat longer on the lower than on the upper side. The tracheal system is conspicuous.

The sensory organs on the pseudocephalon are the same as in the second instar except that they are larger and more pronounced. Those on the eleventh segment also are the same as in the second instar except that they are larger.

THE PUPARIUM

The puparia (fig. 1, B) vary greatly in size, but they average about 7 mm long and 2.5 mm wide. When first formed they are yellowish in color, but in most cases they quickly change to a dark reddish brown. The surface is smooth, although the former segmental lines are faintly visible, and the minute cuticular armature of the third-instar larva can be distinguished under the microscope. The anterior extremity is rounded, the posterior extremity subconical. At the apex there is a small but pronounced rugose elevation which has a longitudinal depression. Just dorsad and on each side of this depression are the rather inconspicuous posterior spiracles. They lie flat against the surface and very close to each other, being separated by no more than one-half their diameter. The anterior spiracles are slightly raised and barely visible to the naked eye. The anus can be seen on the venter at the juncture of the tenth and eleventh segments.

The respiratory apparatus of the pupa has the form shown in Figure 5, C. The prothoracic cornicles are horny structures which protrude from the surface of the puparium just in front of the posterior margin of segment 4. At their distal extremities there are about 12 small openings. The internal spiracle is nearly circular. Its surface is covered with a large number of tiny papillae, which are arranged in double rows radiating out from the central portion.

LYDELLA PINIARIAE

The description of the immature instars of *Lydella nigripes* applies equally well to the same forms of *L. piniariae* with the exception of two minor differences observed in the buccopharyngeal armature of the first-instar larva. A comparison of this structure in the two

species shows that the apex of the anterior hook in *L. nigripes* (fig. 2, B) is distinctly more sharply angled than is the case in *L. piniariae* (fig. 5, B). Occasionally specimens of *L. nigripes* show a somewhat weaker angle, which makes it difficult to separate them from *L. piniariae*, but most specimens are distinct. Another interesting difference between the two species is that *L. nigripes* almost invariably shows a progressive sclerotization of the basal lobes of the buccopharyngeal armature after it is 3 or 4 days old, whereas this never takes place in *L. piniariae*. Occasionally a larva of *L. nigripes* is stunted in growth and the progressive sclerotization does not occur, and at times there is a slight further sclerotization in *L. piniariae*. Nevertheless, in a large number of specimens examined it has been found that this striking difference holds good no matter what host is attacked. In fact, this progressive sclerotization was the rule in a large number of *L. nigripes* larvae dissected from *Bupalus piniarius* that had been attacked at the laboratory, while in every instance where *L. piniariae* larvae were taken from *Porthetria dispar*, *Nygmia phaeorrhoea*, or any other host the maximum progressive sclerotization was negligible.

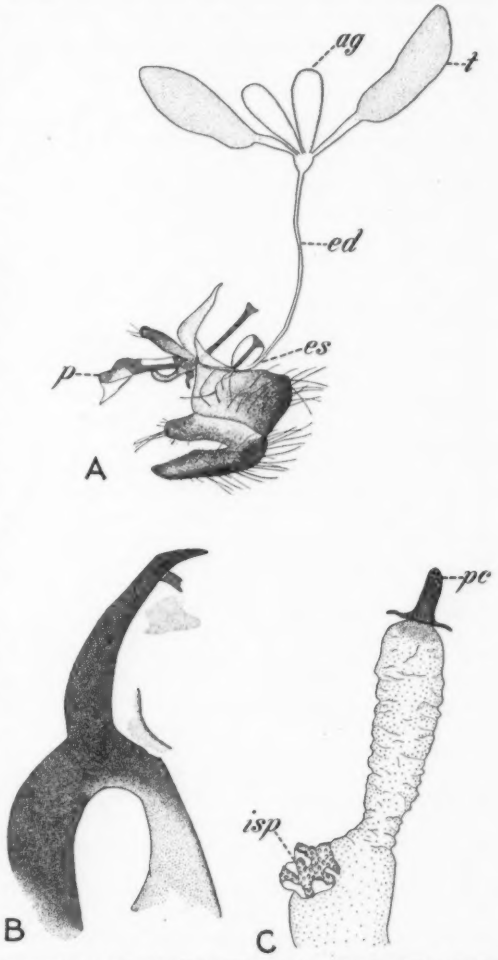

FIGURE 5.—A, Reproductive organs of male *Lydella nigripes*; *t*, testis; *ag*, accessory gland; *ed*, ejaculatory duct; *es*, ejaculatory sac; *p*, penis; B, buccopharyngeal armature of first-instar *L. piniariae*; C, pupal respiratory apparatus of *L. nigripes*; *pc*, prothoracic cornicle; *isp*, internal spiracle

In no other respect could a difference in the immature instars of these two species be determined.

BIONOMICS

SEASONAL HISTORY

LYDELLA NIGRIPES

The seasonal history of *Lydella nigripes* is clearly indicated by field collections and laboratory rearing. It spends the winter as a larva within the mid-gut of the host pupa or host larva. It completes development, issuing from the host and forming its puparium the latter half of April or early in May. *Porthetria dispar* and *Nygmia phaeorrhoea* must be among the first hosts attacked by the first-generation flies, for puparia are recovered from these species the last week in May and early in June. The first second-generation flies issue from these puparia by June 15 and are ready to attack some other host by the end of June. The writer has not recovered puparia of the next generation from field-collected material, but laboratory records indicate that a third generation of flies would appear in the field about the 1st of August. These flies may deposit maggots which hibernate or which complete development. The first host larva attacked in the laboratory, and in which the parasite hibernated, was *Abrostola tripartita*, larviposition occurring on September 3. Probably most of the maggots deposited by the third-generation flies complete development and produce a fourth generation in the first half of September. The writer has made one field recovery of a puparium formed on August 25 from which a fly issued on September 8. The maggots deposited by the fourth-generation flies live through the winter in the hibernating host, or, if they complete development and issue, produce flies so late in the season that they perish without finding host larvae to attack. The writer has made only one field recovery of overwintering *L. nigripes*. This specimen was reared from a pupa of *A. tripartita* the larva of which was collected on October 3. A fairly large percentage of maggots that were deposited in the laboratory at about this time passed the winter within their hosts. Dissections of hibernating stock showed that most of the parasites hibernated as second-instar larvae, but a few specimens remained in the first instar. All the hosts hibernated as pupae with the exception of *Trichiocampus viminalis*, which spun a cocoon and passed the winter as a larva.

LYDELLA PINIARIAE

The location of the laboratory made it difficult to conduct field observations on *Lydella piniariae*. The winter is spent as a first-instar larva in the mid-gut of the *Bupalus piniarius* pupa. Development is completed in the spring, and in the material reared by the writer puparium formation was at its maximum about May 27. The first adults from these puparia appeared about June 10, and some females were ready to larviposit by June 20. Under field conditions, however, the females are not ready to larviposit so early as this. Steiner (*14*) found that maximum issuance of Bupalus adults occurred on June 7, whereas maximum issuance of Lydella females did not occur until July 2. Eidmann (*5*) also notes that *L. nigripes*

(= *piniariae*) issued several weeks after *B. piniarius* moths were in flight. Lydella females issuing July 2 would be ready to larviposit about July 12, and at this time there are probably young *B. piniarius* in the forest which are large enough to be attacked. At least the writer collected larvae in Austria on July 20 that were easily parasitized in the laboratory, and on the 26th of July 50 field-collected *B. piniarius* larvae were dissected and 2 first-instar *L. piniariae* were found. In *B. piniarius* larvae attacked at the laboratory the maggots did not develop beyond the first instar until the following spring. The species therefore completed but one generation in this single-brooded host. It is believed that this is also the case in nature, for Plotnikov (*11*) found first-instar larvae in August and September, and although the present writer has dissected a large number of the parasites from *B. piniarius* larvae collected as late as September 17, he has never found any which were developed beyond the first instar.

Possibly *Lydella piniariae* occasionally develops a summer generation in some other species of host. There would be ample time for a generation to develop and still allow the new flies to attack *Bupalus piniarius* larvae in the fall. A large number of host species have been attacked at the laboratory and in two instances a summer generation has been reared. In one of these a larva of *Tortrix dumetana* attacked on August 6 produced a puparium on August 27, and in the other a larva of *Abrostola tripartita* attacked on July 16 produced a puparium on August 19. Eidmann (*5*) also notes rearing a summer generation of Lydella from *Hematurga atomaria* L., but, not having seen Eidmann's specimens, the writer questions whether the flies were *L. nigripes* or *L. piniariae*. However, the large number of host species attacked at the laboratory in which the parasite larvae did not develop beyond the first instar indicate clearly that development of a summer generation is an exception to the rule.

Everything considered, it is probable that *Lydella piniariae* usually has but one generation a year on *Bupalus piniarius*, and only occasionally passes through a summer generation on some other host.

LENGTH OF LIFE

Lydella nigripes

The flies are sturdy and long-lived under laboratory conditions, where from 5 to 10 are kept in glass-covered wooden boxes 15 by 20 by 10 cm (5.9 by 7.9 by 3.9 inches). As many as 25 may be kept successfully in larger wooden cages (18 by 25 by 20 cm or 7.1 by 9.8 by 7.9 inches) having glass fronts and cloth backs. The flies are fed on lump sugar and a solution of 1 part of honey to 5 parts of water held on sponges. The honey solution is prepared fresh each day. When the flies are not being used they are kept in the dark and, if possible, in a cool place. Table 4 shows the records of a few flies. The flies given only water were held during October and probably survived much longer than they would have if the weather had been warmer.

TABLE 4.—*Length of life of Lydella nigripes flies held in the laboratory*

Flies used	Flies	Minimum life	Maximum life	Average life
	Number	*Days*	*Days*	*Days*
FLIES FED SUGAR AND HONEY SOLUTION				
Mated females used a little for reproduction at laboratory	22	13	66	43.4
Males used in mating cages	12	12	52	38.9
Unmated females	11	50	89	73.7
FLIES GIVEN NOTHING BUT WATER ON SPONGES				
Unmated females	5	5	13	9
Males	5	5	9	6.5

LYDELLA PINIARIAE

Although fewer records were kept on length of life for *Lydella piniariae* than for *L. nigripes*, the records show that the former live just as long as the latter under laboratory conditions.

REPRODUCTIVE SYSTEM

Careful study revealed no difference in the reproductive systems of *Lydella nigripes* and *L. piniariae*.

The external female reproductive organs have been described briefly by Townsend (*17*). On the venter of the last abdominal segment is a long, heavily sclerotized curved sheath, into the base of which the ovipositor fits and which tapers to a microscopically sharp point. With this organ the female punctures the skin of the caterpillar and introduces the living maggot underneath. Pantel (*10*) and Townsend (*18*) have described the same apparatus in detail in *Compsilura concinnata*, a closely allied species.

The internal organs of the unmated female are shown in Figure 6, A. Each ovary is composed of several tubules (fig. 6, B), the number varying with the size of the fly and also often varying slightly in the two ovaries of the same fly. A very small fly may have only 8 tubules and a very large fly 16, whereas an average-sized fly has from 11 to 14. By dissection one can plainly see the outlines of the eggs forming in the tubules at the time the fly issues. Six eggs have repeatedly been counted in a tubule of a freshly issued female and, since this would make from 132 to 168 eggs in an average-sized fly, which is about the number of larvae one finds after development is complete, probably no more eggs are formed. When the fly issues there is one well-developed egg at the base of each ovarian tubule. Those behind it are increasingly small and less developed. As the fly gets older the eggs become larger and more mature, increasing the size of the ovaries.

After the fly is mated the eggs develop rapidly. The mature ones are pushed into the oviducts and pass the spermathecal opening, where they are fertilized, and from there to the uterus, where at first they lie in an even row. The uterus, which is short in the unmated female, gradually lengthens as the eggs descend into it. When full of eggs it consists of four coils within the fly's abdomen. Figure 6, C, shows the reproductive organs of a fly six days after fertilization. Embryonic development progresses rapidly as the eggs descend in

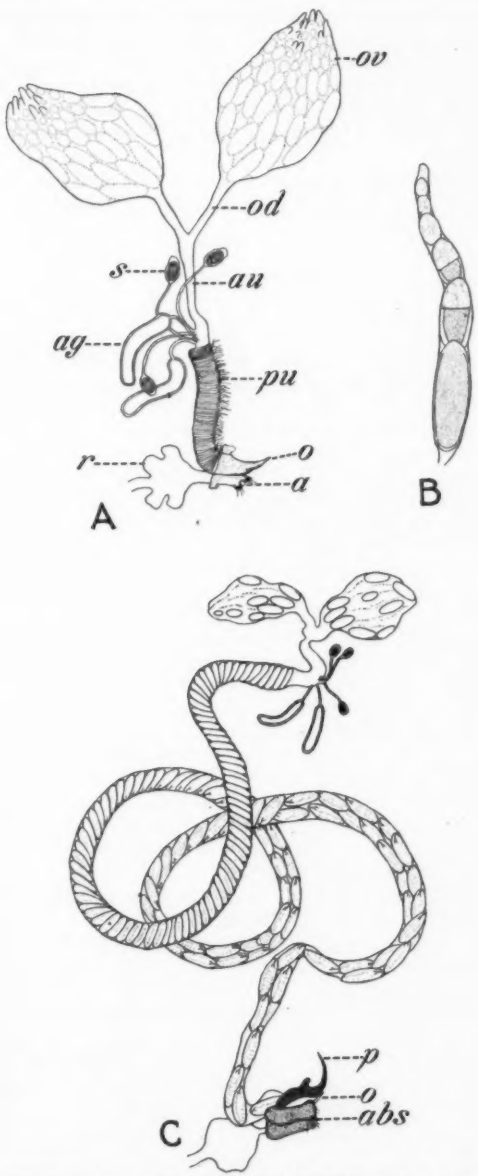

FIGURE 6.—Reproductive system of female *Lydella nigripes*: A, Unmated female with piercing organ removed; *ov*, ovary; *od*, oviduct; *au*, anterior uterus; *s*, spermatheca; *ag*, accessory gland; *pu*, posterior uterus; *o*, ovipositor; *r*, rectum; *a*, anus; B, ovariole; C, mated female six days after fertilization, showing piercing organ in position; *p*, piercing organ; *o*, ovipositor; *abs*, sixth abdormal sternite

the uterus. Those at the posterior end are ready to be deposited while those at the anterior end are as yet undeveloped.

In unmated females the pressure of the growing eggs is eventually great enough to force them into the oviducts and then into the uterus.

In a freshly issued fly the abdominal cavity is filled with a large number of fat bodies. These are gradually absorbed by the developing eggs.

The male reproductive organs are shown in Figure 5, A. As the flies become older the testes seem to shorten somewhat.

MATING

LYDELLA NIGRIPES

Male *Lydella nigripes* do not mate readily until they are a day or two old, but the females mate best when freshly emerged. This peculiarity is well taken care of in nature, for the majority of males invariably issue two or three days before the majority of females. After the females are 2 days old, it is difficult to mate them in the laboratory, and as they get older they resist the males more and more.

In experiments to determine the maximum age at which females might be mated, 6-day-old females were taken in coitu and dissected a few days later. Two of these were apparently fertilized normally. The third had 16 infertile eggs in the lower part of her uterus. These had all been so crowded against the walls by the fertilized eggs behind them that it is believed maggots would have been deposited as usual. Probably ovarian development had forced these infertile eggs past the spermathecal opening before mating took place.

In the laboratory wooden-frame cages measuring 27 by 27 by 65 cm (10.6 by 10.6 by 25.6 inches), covered with cloth, were used for mating. They were kept in the light but not in direct sunlight. Temperatures from 20° to 26° C. (68° to 78.8° F.) are favorable, although at 26° C. the flies are somewhat too active. The morning hours, which are the hours of emergence, are the best for mating.

One female was observed to be mated before her wings were spread. So many males were attracted to this female that it seems possible that such fresh specimens are often fertilized in nature.

The average length of time spent in coitu by 17 pairs was 32 minutes, with a minimum of 14 and a maximum of 48. In one instance a pair disturbed after 29 minutes separated, but 5 minutes later returned and mated for 20 minutes longer.

Female flies never mated more than once, but observation showed that a single male might mate as many as twenty one times and fertilize most of the females. Table 5 shows the record of a male kept at the laboratory. This male was able to fertilize as many as 13 females normally. After that the percentage of infertile eggs rose rapidly, but the eighteenth female, which was mated several days later than the seventeenth, had the normal number of eggs fertilized. Unfortunately the nineteenth female escaped.

TABLE 5.—*Mating record of one male Lydella nigripes in the laboratory*

Date	Number of female fly mated	Time spent in coitu	Eggs found in uterus of female[a]		Date	Number of female fly mated	Time spent in coitu	Eggs found in uterus of female[a]	
			Fertile	Infertile				Fertile	Infertile
		Minutes	*Number*	*Number*			*Minutes*	*Number*	*Number*
June 21	1				June 27	12			
22	2				27	13	23	138	2
23	3		123	7	27	14	25	95	[b] 38
24	4		126	16	28	15		59	[b] 10
24	5				29	16		39	[b] 37
25	6		84	2	29	17	34	68	[b] 73
25	7		141	1	July 2	18	26	106	4
25	8		169	1	2	19			[c]
26	9	20	92	1	3	20		None.	All.
26	10	23	163	2	7	21		None.	All.
26	11	22	120	0					

[a] Determined by dissection.
[b] As these flies were used some for reproduction, the total number of eggs is incorrect.
[c] Fly lost.

LYDELLA PINIARIAE

The observations noted above for *Lydella nigripes* were found to be the same in *L. piniariae*. The number of times that a male could successfully mate was not determined in such detail, but it was found that one male could fertilize eight females normally and if other females had been available this number would undoubtedly have been increased.

CROSS MATING

Experimentation on cross-mating *Lydella nigripes* and *L. piniariae* threw considerable light on the difference and also on the close relationship between the two species. It was very difficult to mate the two species, for they showed little interest in each other and in all pairing the females struggled so violently that it is doubtful whether such mating would take place in nature.

The experimentation on this phase of the work is described below:

Female Lydella nigripes mated with male L. piniariae.—Five females were mated. They were all apparently normally fertilized. A large number of favored-host larvae were attacked and 23 puparia were formed. Flies issuing from these puparia (first-generation progeny of cross) were kept together and six of the females were mated. These females did not attack favored-host larvae well, but 116 larvae were finally attacked. Reproduction was very poor, and dissection of the females revealed that they had been poorly fertilized. The results of dissecting the six females after they had been used as much as possible in attacking host larvae are shown in Table 6.

TABLE 6.—*Relative numbers of fertile and infertile eggs in uterus of six first-generation female progeny of female Lydella nigripes and male L. piniariae*

Female fly No.	Fertile eggs	Infertile eggs	Female fly No.	Fertile eggs	Infertile eggs
1	6	92	4	10	98
2	8	98	5	26	130
3	5	81	6	1	100 plus

Only 5 puparia were secured from the 116 host larvae attacked. Attempts to mate the flies (second-generation progeny of cross) which issued were unsuccessful. It was late in the season and the flies issued over a long period.

Male Lydella nigripes mated with female L. piniariae.—Five females were mated, and all were apparently normally fertilized. A number of host larvae were attacked, but only one puparium was secured. A female fly (first-generation progeny of cross) issued from this puparium.

It is not surprising that so little success was obtained with this cross, for *Lydella piniariae* was exceptionally difficult to rear in the laboratory. Attempts to rear *Bupalus piniarius* larvae for attack gave poor results, very few pupae being brought through the winter.

Female fly, first-generation progeny of cross between male Lydella piniariae and female L. nigripes, mated with male L. nigripes.—No larviposition was secured from this female. Dissection showed that only eight eggs were fertilized.

Female fly, first-generation progeny of cross between male Lydella nigripes and female L. piniariae, mated with male L. nigripes.—This female practically refused to attack host larvae. Dissection showed 15 fertile and 150 infertile eggs in her uterus.

The results of these experiments indicate a very close relationship between the two species, for mating was secured between them and females of both crosses were fertilized. The experiments indicate, nevertheless, that the two flies are probably different species. Mating was so difficult that it could hardly occur in nature, and there was a very high percentage of sterility among the progeny resulting from such mating.

PERIOD BETWEEN MATING AND LARVIPOSITION

Howard and Fiske (7) note that only three or four days are required for the adult female *Lydella nigripes* to reach sexual maturity. The writer was not able to duplicate this record. His experiments showed that the time between the mating of the flies and the first larviposition in both *L. nigripes* and *L. piniariae* may be as short as six days in very warm weather, but even then the flies did not larviposit eagerly for a few more days. If the weather is cooler, a day or two more is necessary.

LARVIPOSITION

A number of different ways of presenting caterpillars to larviposting flies were tried in the laboratory. The most successful larviposition was secured in wooden boxes measuring 15 by 20 by 10 cm (5.9 by 7.9 by 3.9 inches) and having glass covers. Ten or fifteen larvae were placed in such a box with four or five flies. The box was kept in the light, and as the host larvae were attacked they were removed with a light brush through a hole in the side of the box. Another fairly satisfactory container for this purpose was a wooden box having a glass front and a cloth back. The cloth back was turned toward the light and both caterpillars and flies remained on the cloth fairly well. In both containers it is advisable to keep the larvae in motion.

Lydella nigripes

During the summer months females of *Lydella nigripes* attacked a large number of larvae of different species at the laboratory. Attack was fairly good but decidedly erratic. Hairless larvae were always more readily attacked than hairy ones. It was often very difficult to get *Porthetria dispar* larvae attacked, but there was never the slightest difficulty, under proper conditions of temperature, in having many species of naked larvae parasitized. The optimum temperature for larviposition is between 25° and 30° C. (77° and 86° F.) Flies which refused to larviposit at 21° C. (69.8° F.) did well at 25° C., but the best results ever obtained when using *P. dispar* larvae were at 30° C., when five females deposited in 41 larvae in one and one-half hours.

The fly larviposits by a quick downward and forward movement of the piercer, which breaks the skin of the host larva and allows the larvipositor to enter and deposit the small parasite maggot. A moving caterpillar immediately attracts a fly wishing to larviposit. She quickly runs after it, approaching from the side. Suddenly, with a quick jump forward, she inserts the piercer and larvipositor into the side of the caterpillar and then either passes over it to the other side or flies away. The whole thing is done so quickly that it often seems to be a single motion forward. Often the fly appears to be unsuccessful in her first attempt to larviposit, for she turns around and approaches the larva from the other side. Occasionally as a caterpillar is struck it falls and then the fly falls with it. Sometimes a fly is attracted to a motionless caterpillar and attacks it immediately.

A drop of liquid may exude from the host larva at the point of attack, and the fly often hunts for this liquid and eats it. This is particularly true when larvae of *Bupalus piniarius* and also of *Cadonia punctoria* L., another geometrid, are parasitized. As a rule the fly pays no attention to a larva of *Porthetria dispar* after attacking it.

Species of Vanessa larvae, when confined with flies, often strike at them and sometimes smear them with a green regurgitated liquid. This causes the fly to tremble all over and run hither and thither in a crazy manner for several seconds, or even a minute, after which the fly is again normal.

The young maggots are deposited posterior end first. In one or two instances observed the host larva's skin was so thick that it was not completely punctured and the maggot was left partly protruding. In these cases the parasite was not able to gain entrance into the host.

Lydella piniariae

Great difficulty was experienced in getting *Lydella piniariae* females to attack any hairy larvae. All naked larvae, however, were eagerly attacked. Even large geometrid larvae and species of Smerinthus larvae, which have skins much too thick for the piercer to penetrate, were eagerly attacked in an attempt to larviposit.

It was particularly desirable to get *Lydella piniariae* to larviposit in *Porthetria dispar*, *Nygmia phaeorrhoea*, and *Vanessa urticae* L. in order to compare its larval development in these hosts with that of *L. nigripes*. Considerable time was therefore spent with these host larvae. Flies of all ages were tried on all larval instars of the hosts. By using larvae with as little hair as possible (in *P. dispar* large third-instar larvae and in *N. phaeorrhoea* fourth-instar larvae) and

by using flies kept continuously in the light, a little larviposition was obtained. The flies would usually run around the cages, over and around the larvae, for hours before they would suddenly attack one.

The *Lydella piniariae* female larviposits in practically the same manner as does *L. nigripes*. She is very apt, though, to jump on a larva, run up and down its back, and larviposit by a movement which shoves the abdomen downward and forward, as if she were sitting down on the larva. The fly shows remarkable ability in staying on a larva, but if the violent motion shakes her off she returns immediately until satisfied.

REPRODUCTIVE CAPACITY

The number of larvae deposited by females of both *Lydella nigripes* and *L. piniariae* varies greatly according to the size of the fly. In one very small fly only 65 maggots were produced, while the largest number found was 171 in a very large fly. *L. piniariae* obtained from host larvae collected in the field are a little larger than *L. nigripes* reared from field-collected *P. dispar*.

LARVAL DEVELOPMENT

LYDELLA NIGRIPES

Embryonic development is complete in *Lydella nigripes*. When a larvipositing female is dissected, the first-instar maggots can be seen actively moving inside their eggshells. At the posterior end of the uterus they are large enough to fill the egg, while at the anterior end they are rather small. It is believed that the act of larviposition usually slips off the delicate eggshell as the larva is forced into the host, for dissections immediately after larviposition almost invariably show larvae outside of the egg membrane. Occasionally, however, an unruptured egg is found.

Immediately after deposition the larva works its way into the cavity of the mid-gut of the host, larvae having been observed in this position five minutes after the host larva was attacked. The parasite larva may attach itself to the wall of the gut by its stigmatic hooks, being thus fastened by its extreme posterior tip with the rest of the body lying free within the gut, or it may enter the gut completely and float freely in the liquid that is found there. About as many larvae have been observed in one position as in the other. The larva may attach itself as it bores through the wall of the gut or later. This point was not determined. Usually, perhaps always, the attachment is at a point where the anal spiracles lie against one of the host's tracheae, and it is believed that the parasite larva may get a supply of air in this way. Nevertheless, the larvae that float freely within the gut surely have no direct contact with the air, and it may be that the tracheal system in this instar is not functional, the peculiarity of attachment being simply the survival of a now nearly extinct habit, at one time useful.

The first-instar larva feeds on the partly digested contents of the host's mid-gut. It usually grows rapidly, but if the food supply is scarce development may proceed quite slowly. The larva measures from 0.90 to 1.28 mm when first deposited. By the time it is 1.40 mm long, usually three or four days later, it invariably shows evidence of the progressive sclerotization of the basal region of the buccopharyn-

geal armature mentioned earlier (p. 970). The first larval instar is completed in the mid-gut of the host; the second instar is also often fully completed and the skin cast either in the position of attachment or while still floating free in the contents of the mid-gut. The well-developed second-instar larva sometimes bores through the gut to get more food. The third instar is spent outside of the gut, with the larva voraciously feeding on the contents of the host's body cavity. This instar completes its development rapidly. Usually the fully developed *Lydella nigripes* larva issues from the host larva. Occasionally the host pupates before development of the parasite larva is complete, but then it issues readily from the pupa. Issuance is made at any convenient point. The larva cuts a hole with its mouth hooks, emerging head first. A few cases have been noted where the parasite, instead of issuing, forms the puparium within the dead host's skin or pupal shell.

More than one *Lydella nigripes* can develop in the same host larva. In one instance three developed in a single *Porthetria dispar* caterpillar, and once seven normal-sized puparia were obtained from a single larva of *Polia brassicae*.

The time spent in each larval instar varies considerably according to the temperature, size of host, etc. A few specimens were dissected each day to determine growth. The quickest development noted was in *Vanessa urticae* larvae attacked in the laboratory on July 5. Four days were spent in the first instar, 3 in the second, and 3 in the third. Other records showed that 50 days were required for larval development in retarded *Porthetria dispar* larvae that were attacked on August 28.

After leaving the host, the third-instar larva burrows into the ground a short distance to form its puparium. In the laboratory the puparium is readily formed without earth or other covering material. It is believed, however, that in nature the larvae always enter the ground, for when given an opportunity in laboratory experiments they always do so. Ten larvae placed on rather firmly packed soil in the laboratory burrowed down to an average depth of 3.1 cm (1.2 inches), with a maximum of 4.0 cm (1.6 inches) and a minimum of 1.0 cm (0.4 inch). Outdoors six larvae burrowed to an average depth of 1.2 cm (0.5 inch), with a minimum of 0.6 cm (0.2 inch) and a maximum of 1.8 cm (0.7 inch). Before forming their puparia, all the larvae under observation turned around so that they lay with their heads pointed upward.

Lydella piniariae

Larval development in *Lydella piniariae* is slightly different from that in *L. nigripes*. Hatching and entrance into the mid-gut of the host are the same, but in *L. piniariae* the larva always attaches itself to the intestinal wall and it never shows progressive sclerotization of the basal lobes of the buccopharyngeal armature. The first-instar larva of *L. piniariae* develops so slowly that it passes the winter in this stage within the host pupa. Possibly the reason the larva always attaches itself to the wall of the gut is that it spends such a long time in this position that provision must be made for an air supply.

Development in the spring seems to follow no definite rule. Sometimes the parasite cuts two openings in the host's gut, one near the

parasite's anal spiracles and the other near its mouth, and holds a mass of the host's body material in a rather firm lump at each of these points. These masses are full of tracheal tubes, and at the posterior end of the parasite's body many of them are held by the stigmatic hooks. The larva feeds on the mass of material held anteriorly. At other times the gut is ruptured at only one point, and one larva was observed which had reached the second instar without puncturing the gut at all. In general, though, the gut is punctured at the end of the first or at the beginning of the second instar, and as the larva feeds it surrounds itself with a brownish, filmlike protective covering of host remains. The second-instar larva is also attached to one of the host's tracheae. The third-instar larva is inclosed in a protective covering or sac as before, but it has never been observed attached to a trachea. There is so much variation in dissected material that it was impossible to determine accurately the duration of the second and third larval instars, but development is probably rather slow in nature, for puparia do not appear from collected pupae until the latter part of May or early in June.

It is not uncommon to find more than one *Lydella piniariae* maggot in a *Bupalus piniarius* larva in the fall, but the writer never reared more than one parasite larva from a host pupa in the spring, and dissections of pupae never showed more than one present, except in one instance, where there were two third-instar larvae, one of which was dead. Apparently a larva of *L. piniariae* is always able in some way to eliminate competitors of the same species. Marks have been noted on dead larvae that were undoubtedly made by the mouth hooks of another.

When feeding is completed, the larva leaves the host and burrows into the ground as was noted for *L. nigripes*.

PERIOD SPENT IN THE PUPARIUM

LYDELLA NIGRIPES

Data on the period of time between the formation of the puparium and the issuance of the flies were obtained from laboratory-reared material. As the puparia were formed, they were isolated and then examined daily for issuance of flies. Table 7 shows the results obtained.

TABLE 7.—*Time spent by Lydella nigripes in the puparium*

Time of formation of puparium	Puparia producing male adults	Puparia producing female adults	Average time spent in puparium	
			Males	Females
	Number	*Number*	*Days*	*Days*
Apr. 25 to May 1	12	10	17.5	17.9
May 31 to June 5	14	10	12.3	12.6
July 1 to 15	1	3	13.0	12.3
July 16 to 31	42	55	11.9	12.8
Aug. 1 to 15		1		14.0
Aug. 16 to 31	2	8	12.0	14.7
Sept. 1 to 15	20	28	12.2	14.0
Sept. 16 to 30	56	89	15.7	16.8
Oct. 1 to 15	7	4	19.0	25.0
Oct. 16 to 31	3	2	26.0	31.0

The time spent in the puparium varies greatly with the temperature. Male adults issue in from 12 to 14 days in June, July, and August, but in October as many as 26 days may be required. Females require a day or so longer. This peculiarity is common among the Tachinidae, and undoubtedly is an important factor in mating, for the best mating is secured between freshly emerged females and males from 2 to several days old. When a number of *Lydella nigripes* pupae are secured from simultaneously attacked host larvae, the first-formed pupae always produce a large percentage of males and those formed later a large percentage of females.

Toward the end of the rearing season the majority of flies that issued were females. One case was noted where 17 larvae of *Polia brassicae* attacked between August 25 and September 4 produced 33 puparia between September 6 and 19, and from these puparia 12 male and 21 female *Lydella nigripes* flies issued. It would be almost impossible to check such results in nature, but the phenomenon might be a natural one, for we know that males mate several times, and there is therefore less need for equal numbers of each sex toward the end of the summer.

Lydella piniariae

The length of time *Lydella piniariae* spends in the puparium was also observed under laboratory conditions. The puparia were part of a large number secured from overwintering *Bupalus piniarius* pupae. The time was found to be about the same as for *L. nigripes*. The fact that the majority of male larvae complete development earlier in the season than the females is clearly brought out in Table 8.

Table 8.—*Issuance of Lydella piniariae flies from two lots of puparia*

Time after formation of puparia (days)	From a lot of 540 puparia formed May 24, 1929		Time after formation of puparia (days)	From a lot of 211 puparia formed June 4, 1929	
	Adult males issuing	Adult females issuing		Adult males issuing	Adult females issuing
	Number	*Number*		*Number*	*Number*
14	110		14	14	
15	120		15	22	18
16	115	10	16	7	70
17	33	49	17		46
18	3	20	18		2
19		2	19		3

LABORATORY REARING

Lydella nigripes

Lydella nigripes was reared at the laboratory on retarded *Porthetria dispar* in order to get material for study. A large number of other hosts were also exposed to attack, in an attempt to get data on the different host species in which it could develop. The species in which *L. nigripes* was reared are listed earlier in this paper (page 965). Development in *P. dispar* larvae was rapid in most cases, but there was considerable variation in the time spent as a larva. In *P. dispar* stock attacked the latter part of August, many of the parasite larvae developed very slowly and a few of them did not develop

beyond the first instar. It is believed that the retarded host larvae did not give sufficient nourishment to the parasites, for, with the exception of *Bupalus piniarius*, development was rapid in other hosts attacked at this time. This species can hardly be compared with the others, however, for most of the larvae were so small when attacked that development was retarded. Furthermore, in practically every case *L. nigripes* completed development in *B. piniarius*. *L. piniariae*, on the other hand, never developed beyond the first instar in this host, during the summer. *L. nigripes* larvae always showed the progressive sclerotization of the basal lobes of the pharyngeal armature after they had developed in *B. piniarius* larvae for a few days, but this never occurred in *piniariae* larvae.

The smallest *Porthetria dispar* larvae successfully attacked at the laboratory were large second-instar caterpillars.

Lydella piniariae

Results from attempts to rear *Lydella piniariae* larvae at the laboratory were very different. A fairly large number of hosts were attacked and they include many species in which *L. nigripes* completed a summer generation. Nevertheless, the only evidence obtained which indicated that a summer generation of *L. piniariae* might develop, was one puparium formed on August 27 from a pupa of *Tortrix dumetana*, the larva of which was attacked at the laboratory on August 6, and one puparium formed August 19 from a larva of *Abrostola tripartita* attacked July 16. A list of larvae attacked by *Lydella piniariae* follows. Those starred (*) are species in which *L. nigripes* develops a summer generation.

*2	*Abrostola tripartita* Hufn.	*53	*Nygmia phaeorrhoea* Donovan.
2	*Agrotis pronuba* L.	1	*Pieris brassicae* L.
1	*Amphidasis betularia* L.	6	*Pieris rapae* L.
*25	*Bupalus piniarius* L.	*2	*Plusia gamma* L.
*7	*Calophasia casta* Bkhn.	*225	*Porthetria dispar* L.
43	*Cadonia punctoria* L.	2	*Smerinthus quercus* Schiff.
2	*Diphthera alpium* Osbeck.	*4	*Synopsia sociaria* Hbn.
1	*Drymonia querna* Fab.	8	*Tortrix dumetana* Freyer.
*38	*Polia brassicae* L.	81	*Vanessa urticae* L.
9	*Melitaea* sp.	3	*Vanessa io* L.

In general the larvae attacked lived a long time. Most of them lived long enough for the parasites to develop, but dissection of the stock showed that the parasite larvae did not develop beyond the first instar. Two first-instar larvae were found in *Porthetria dispar* caterpillars 18 days after larviposition, two first-instar larvae were found in *Nygmia phaeorrhoea* larvae 17 and 24 days after attack, and one first-instar larva was found in *Vanessa urticae* 17 days after larviposition. These facts indicate that as a rule *Lydella piniariae* does not develop beyond the first instar in the summer, but is essentially a single-brooded species. The two exceptions noted indicate that the species may occasionally have a summer generation.

COMPARISON OF LYDELLA NIGRIPES REARED FROM PORTHETRIA DISPAR AND FROM NYGMIA PHAEORRHOEA

Puparia of *Lydella nigripes* were obtained the last part of May and the early part of June, 1930, from field-collected larvae of *Porthetria dispar* and *Nygmia phaeorrhoea*. In order to avoid any possible con-

fusion between flies reared from these two hosts, the material originating from *P. dispar* and that originating from *N. phaeorrhoea* were kept separate for the entire season. Material was cross-mated in both directions with no difficulty, and the progeny resulting from both crosses were reared for three generations. No difference was noted in the larvae or adults reared from the two hosts or from cross-mated stock.

COMPARISON OF LYDELLA NIGRIPES WITH COMPSILURA CONCINNATA

Although the adults of *Lydella nigripes* and *Compsilura concinnata* show morphological differences, the similarity in their biology and immature stages has been noted in several instances. Townsend (*17*) in 1908 and Pantel (*10*) in 1910 first called attention to this, and Howard and Fiske (*7, p. 296*) in 1911 noted that Lydella has a more restricted host relationship than Compsilura and "is exceedingly rare as a parasite of the gipsy-moth caterpillars," but "in every other respect except host relationship, the habits of the two are identical, and so far as known the earlier stages are absolutely indistinguishable."

So far as host relationships are concerned, it is true that, in spite of the large number of hosts which Lydella attacks, the number which Compsilura is known to parasitize is far greater. *Lydella nigripes*, however, may at times be of some importance as a *dispar* parasite.

It seemed worth while to try again to detect differences between the immature stages of the two parasites. No way of separating the first-instar larvae was found, but those of the second and third instars, as well as the puparia, are quite distinct. The anterior spiracles of second-instar *Lydella nigripes* larvae almost invariably have 3 papillae, rarely 2, and very seldom 4. In Compsilura, on the other hand, there are almost always 6 or 7 papillae. In only one instance has an exception, where there were 5, been noted. The third-instar larvae may also be separated by the number of papillae of the anterior spiracles. In Lydella there are 3 or 4, in Compsilura 5 to 7. The species may further be distinguished in this instar by the arrangement of the cuticular spines surrounding the posterior spiracles. In Lydella there are 2 small patches of spines which coalesce at their bases, situated just anterior to the posterior spiracles, and 1 or 2 similar patches placed close together posterior to the spiracles. In Compsilura one finds rather heavy spines, but they do not coalesce at their bases into patches. The puparia are distinct. In *Lydella nigripes* the posterior end is somewhat pointed, the spiracular plates are nearly contiguous, and the area just below them is distinctly raised. The posterior end of the *Compsilura concinnata* puparium is rounded, the spiracular plates well separated, and the area below them practically flush.

These differences, although important aids in the determination of the immature forms, do not alter the fact that the two species are biologically very closely related. The habits of the flies—larviposition, larval development, and seasonal history—are all so nearly identical that one is amazed that Compsilura became so easily and widely established in North America, while, so far as known, Lydella with the same opportunities could not become acclimatized. The reasons for this remain a mystery, but one or two points noted in

studying the flies may be interesting in this connection. In the first place there is a very marked difference in the way the two species larviposit. *Compsilura concinnata* eagerly attacks almost any species of host larva whether it is hairy or not. The flies attack with such vigor that they easily puncture the skin with their sharp piercers and deposit their maggots. Flies of *Lydella nigripes*, on the other hand, do not attack hairy larvae at all eagerly; in fact, the attack is often not aggressive enough to push the piercer through the host larva's skin. They seem quickly discouraged or tired and soon can not be induced to attempt larviposition at all. Another, perhaps even more important, difference is the fact that Compsilura larvae usually survive better than those of Lydella. General laboratory rearing of these parasites in larvae of *Porthetria dispar* and *Nygmia phaeorrhoea* showed that invariably a high percentage of the larvae attacked by Compsilura gave puparia, while even the larvae which were surely attacked by Lydella (as evidenced when a drop of liquid exuded at the point of attack) produced a low percentage of puparia. The reasons for this could not be determined. Dissections almost always showed healthy larvae, although occasionally none could be found. A third consideration which might help explain why *Compsilura concinnata* is so successful in America whereas *Lydella nigripes* has not become established is that of competition. The two species must be severe competitors in nature. In Europe, it is true, they exist side by side, although apparently neither ever reaches a very high degree of effectiveness as a parasite.

In North America *Compsilura concinnata* is very successful. It has perhaps been able to fill its place in the American fauna so well that *Lydella nigripes*, which must compete for nearly the same place, can not establish itself.

Laboratory experiments on the competition between *Compsilura concinnata* and *Lydella nigripes*, as indicated in the following section, seem to show that *Compsilura concinnata* is the stronger of the two, but in a number of instances both parasites developed in the same host larva.

COMPETITION WITH OTHER PARASITES

LYDELLA NIGRIPES

No data were secured in the field regarding the competition between *Lydella nigripes* and other parasites in *Porthetria dispar* or *Nygmia phaeorrhoea*. There might be rather severe competition between *Lydella nigripes*, *Compsilura concinnata*, *Carcelia separata* Rond., *Sturmia inconspicua* Meig., and *Hyposoter* spp. in *Porthetria dispar*, for they all attack and issue from the host about the same time. In *Nygmia phaeorrhoea*, *Lydella nigripes* has *Compsilura concinnata*, *Sturmia nidicola* Townsend, *Pales pavida* Meig., and *Zenillia laxifrons* Villeneuve as severe competitors.

In the laboratory an experiment in competition was carried on between *Lydella nigripes* and *Compsilura concinnata* in *Porthetria dispar* larvae. Third and fourth instar host larvae were used. Such conditions may never occur in the field, but the results are given in Table 9 as having at least an academic interest.

TABLE 9.—*Competition between Lydella nigripes and Compsilura concinnata in third and fourth instar Porthetria dispar larvae attacked at the laboratory*

Parasite	Host larvae attacked	Host larvae from which puparia of the parasite were obtained			
		Compsilura	*Lydella*	*Lydella* and *Compsilura*	Total
Lydella (check)	50		24		24
Compsilura (check)	50	20			20
Lydella and *Compsilura* simultaneously	65	18	11	7	36
Lydella and 2 days later *Compsilura*	63	12	7	1	20
Lydella and 4 days later *Compsilura*	63	6	10	1	17
Compsilura and 2 days later *Lydella*	63	17	3		20
Compsilura and 4 days later *Lydella*	63	40	5		45

LYDELLA PINIARIAE

No data were secured from the field on competition between *Lydella piniariae* and other parasites in *Bupalus piniarius*, but the competition must be very keen, for a large number of hymenopterous parasites are reared from this host.

FACTORS LIMITING THE EFFECTIVENESS OF THE TWO SPECIES AS PARASITES

LYDELLA NIGRIPES

It is rather surprising that *Lydella nigripes*, which is usually present in some numbers in infestations of *Porthetria dispar*, should be of no greater importance as a parasite of that host. There does not seem to be any reason why the species should not be at least potentially as effective as *Compsilura concinnata*. Experimentation seems to indicate, however, a few of the reasons why it does not increase more. Perhaps the most important is that Lydella seems to prefer hairless larvae for attack. If this is as true in the field as it is in the laboratory, it can be understood why *dispar* might be avoided when there was an abundance of preferred host material in the field. The fact that the species is very polyphagous also cuts down its effectiveness as a *dispar* parasite, since it is not obliged to confine its efforts to this host. Another fact that may limit the species is that a large percentage of the maggots deposited in the late fall complete development at such a late date that the issuing flies do not find larvae to attack, and consequently perish without reproducing. In one instance 21 larvae of *Abrostola tripartita* were attacked at the laboratory on October 7. Nine puparia were formed on November 6, from which flies issued about December 10, much too late for them to find larvae to attack. Only four puparia were recovered from the hibernating pupae in the spring. If the same tendency is shown in the field there must be a very high mortality.

Lydella nigripes has generally shown itself a more effective parasite of *Nygmia phaeorrhoea* than of *Porthetria dispar*, but it has the same limitations on this host also.

During this work there was no opportunity to collect *Lydella nigripes* puparia in the field in order to ascertain whether or not the species is attacked by secondary parasites. It spends such a short

time in the immature stages that it is probably not seriously parasitized, but laboratory notes for 1906, 1907, and 1908 indicate that a few *Monodontomerus aereus* Walker were reared from the puparia.

LYDELLA PINIARIAE

Lydella piniariae is much more effective than *L. nigripes*. The percentage of parasitization is often very high, and in every case under the writer's observation it showed a marked increase during the second and third years of the infestation. All the limiting factors that were noted for *L. nigripes* are inapplicable to *L. piniariae*. It eagerly attacks Bupalus larvae, goes into hibernation early in the summer, and probably confines itself almost exclusively to the one host. As a matter of fact, there does not seem to be any reason why the parasite should not go on increasing at the expense of the host at such a rate that it would soon eliminate it, and it is believed that this would actually take place if the combined efforts of the parasites attacking *B. piniarius* did not check an infestation before L. *piniariae* reached its full effectiveness. Of course, there are some rather obvious limiting factors, and one of them may be serious enough to hamper greatly the parasite's effectiveness at times. This is a hyperparasite, *Mesochorus politus* Grav., which attacks the parasite while it is within its host. More than 57,000 *L. piniariae* pupae were reared in 1929, and this secondary parasite was not encountered, but in 1930 out of a lot of 600 puparia no less than 299 adults of *M. politus* issued. Sittowski (*13*) notes that he found this hyperparasite destroying 10 per cent of the *L. piniariae* pupae. A limiting factor of less importance is the fact that only one Lydella larva can develop in a single *B. piniarius* larva. This must result in a rather heavy mortality among the parasites for, of course, one host may be attacked several times. There must also be severe competition between *L. piniariae* and the large number of parasitic species which inhabit *B. piniarius*. The parasite must also suffer greatly when the host pupae fail to live through the winter owing to climatic conditions, fungus, etc.

SUMMARY AND CONCLUSIONS

Lydella nigripes Fallén is a polyphagous tachinid parasite in Europe. Because it is of some importance in controlling the gipsy moth (*Porthetria dispar* L.) and the brown-tail moth (*Nygmia phaeorrhoea* Don.), it seemed desirable to try to establish it in the United States. During the summer it completes three and often four generations in different host species. It hibernates as a second-instar larva within the host pupa or larva.

Lydella piniariae Hartig is an important European parasite of the pine geometrid (*Bupalus piniarius* L.). The host larvae are attacked during the summer and the parasite develops very slowly, hibernating as a first-instar larva in the mid-gut of the host pupa. As a rule the parasite probably completes only one generation each year in this single-brooded host, but a summer generation may occasionally develop in some other host species.

The two species have previously been considered identical, but soon after this study was begun it became apparent that there was a difference in the biology of flies reared from *Bupalus piniarius* and those reared from *Porthetria dispar* and *Nygmia phaeorrhoea*. It was

possible to separate the adults morphologically. The immature stages have been studied and found to be almost identical. The only differences noted were in the first-instar larvae. The buccopharyngeal armature of *Lydella nigripes* shows progressive sclerotization of the basal lobes as the larva becomes fully developed, whereas this does not occur in *L. piniariae*, and the tip of the buccopharyngeal armature in first-instar *L. nigripes* is more sharply angled than in *L. piniariae*.

The adults of *Lydella nigripes* and *L. piniariae* show little difference in behavior. Both are long-lived. They mate readily in the laboratory and the males are capable of mating many times. Experimentation in cross-mating the two species indicated that they probably would not mate in nature. Cross-mated females were fertilized, but the progeny were nearly sterile.

The females of *Lydella nigripes* and *L. piniariae* have a sharp, stout piercer attached ventrally on the last body segment. The base of the ovipositor fits into this instrument and the fly uses it to puncture the host larva's skin. As the skin is punctured a living maggot is deposited inside the host. From 125 to 150 maggots are deposited by average-sized females of both species.

Lydella piniariae practically refuses to attack hairy larvae, whereas *L. nigripes*, although preferring naked larvae, attacks many species of hairy caterpillars.

There are some differences in the larval development of the two species. The first-instar larva of *Lydella piniariae* is always attached to the wall of the host's mid-gut, the second-instar larva is apparently always attached to a host trachea, and the third-instar larva is found in a protective sac or covering formed from the host remains. About as many of the first-instar larvae of *L. nigripes* float free in the liquid contents of the mid-gut as attach themselves to a trachea, many of the second-instar larvae float free in the same position, although some attach themselves to a trachea, and the third-instar larvae may or may not form a protective covering or sac from the host's remains. The mature larvae of both species leave the host and burrow a short distance into the ground to form puparia. The males spend about 11, the females 12, days as pupae.

Lydella nigripes regularly completed a summer generation in larvae of *Porthetria dispar*, *Nygmia phaeorrhoea*, *Bupalus piniarius*, and many other host species attacked at the laboratory. *L. piniariae*, on the other hand, rarely completed a summer generation. In two isolated instances puparia were recovered, but deposited maggots never developed beyond the first instar in *B. piniarius*, *P. dispar*, *N. phaeorrhoea*, or a number of other host species in which *L. nigripes* developed rapidly.

Although there are some marked differences in the life histories and habits of *Lydella nigripes* and *L. piniariae*, there are similarities in almost every phase of their life histories which show that a very close biological relationship exists between them. The obvious explanation is that they present an example of species evolution, which has not progressed far enough to bring about marked morphological changes. Since *L. piniariae* may be considered as simpler than *L. nigripes*, it is probably the older.

A brief comparison was made between *Lydella nigripes* and *Compsilura concinnata*, a parasite of *Porthetria dispar* and *Nygmia phaeor-*

rhoea which has been very successfully established in the United States. The life histories, habits, and immature stages of the two parasites are remarkably similar. The first-instar larvae could not be separated, although slight differences were noted in the later instars. The two species undoubtedly compete severely in nature. In the laboratory *C. concinnata* seems to be somewhat stronger, but larvae of both species often developed in the same host larva. *C. concinnata*, nevertheless, is much more aggressive. It eagerly attacks hairy caterpillars as well as naked larvae. Perhaps this is why *C. concinnata* has been able to establish itself so well in the American fauna while *L. nigripes* has been unsuccessful.

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POROSITY AND WATER ABSORPTION OF FOREST SOILS[1]

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INTRODUCTION

The manner in which water in the form of rainfall or run-off acts upon the surface soil, and the capacity of the soil to absorb water, are well recognized as two interrelated factors that link together all problems of soil erosion, flood control, and water conservation. Two other factors that, less obviously, are linked to these through their effect on surface soils are land abandonment on the one hand and forestry on the other.

In the Central States, where the studies here detailed were pursued, land abandonment has reached disturbing proportions, and the end is not yet. The 1925 census records 6,500,000 acres of idle and fallow

FIGURE 1.—A field that has become a waste of ever-growing ditches

land in these States; and a recent survey of a typical southern Ohio county (*6*)[3] reveals 50 per cent of the improved land abandoned since 1900.

With abandonment of poor land came erosion. Indeed, soil erosion started on the steeper slopes and hills as soon as the forest cover was cleared away, but reached much greater proportions as unproductive fields were abandoned to the elements. The loss from erosion under faulty methods of managing hill lands is doubtless more wasteful and destructive than the loss of plant food through cropping. The surface soil itself is quickly washed away by heavy rains and gullies form and grow until what was once a field becomes a waste of ever-growing ditches. (Fig. 1.)

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[2] Maintained in cooperation with Ohio State University and Ohio Agricultural Experiment Station.
[3] Reference is made by number (italic) to Literature Cited, p. 1014.

The influence of forests and the practice of forestry are all in the other direction of holding and building up surface soils and, perhaps more important, of lightening soil structure and so increasing porosity. Under a cover of forest trees, erosion is not a problem where the forest is not repeatedly burned or severely overgrazed. The tree roots and protective cover of leaf litter keep the soil from washing. The same conditions which prevent erosion favor water conservation. Forest soils protected by tree cover and leaf litter retard the effect of surface run-off and thereby conserve the moisture which is precipitated in the form of rain and snow. This water is then held in storage as a feeder of wells and springs and, slowly released, stabilizes stream flow and tends to check excessive floods.

Thus it is that, whereas problems of floods, erosion, and natural reservoirs are in the Central States largely problems of soil management, one solution, and often the only solution, of such problems lies in putting idle land to work through the growing of protective and productive crops of forest trees.

While the influence of forests and forest litter in the control of the aforementioned problems is recognized, and reforestation of waste land is proposed as one of the important solutions, yet the changes in soil structure, fertility, and moisture content undergone in the transition from forest to field conditions have not been understood thoroughly enough for foresters to appreciate the difficulties in starting new tree growth on waste land.

In order to cope with these conditions, it is necessary for the forester to take advantage of certain soil relationships and to apply some basic facts regarding the soil to the problems of forest management. One approach is through a study of the functions of forest litter.

The literature pertaining to litter, and especially to its effect upon soil porosity and water absorption, is meager. Eiffert (*5, p. 1266–1269*), assuming 0.12 inch of rainfall to be held by the average forest litter, pointed out the insignificance of this amount in its effect on the Mississippi floods. Lowdermilk (*3*) recognized that the absorbing capacity of forest soil as a function of its porosity is to some extent independent of litter cover. McCarthy (*7, p. 102*) emphasized the importance of forest soil structure in influencing water-holding capacity. Munns (*4*) estimated the maximum excess of water held in forest over field soil to be about 1 inch, but stated that with good forest practice this amount might be increased. Korstian (*2*) recognized the difference between litter-covered and bare soils and found the penetrability of litter-covered soil to be 175 per cent greater than that of bare soil. Warington (*8, p. 47*), in commenting on two Rothamsted soils, stated that the soil densities increased to a depth of 36 inches and were fairly constant below that level. Harmer (*1*), when reporting on the densities of six field soils and six open prairie soils, found them about equal in compaction. He stated that the density increased with depth rather gradually in prairie soils, but more rapidly in forest soils.

To arrive at a better understanding of the relation of soil to the problems of forestry and to determine the influence of forest cover and forest litter, a series of studies has been undertaken, out of which the study of soil porosity and capacity for water absorption was chosen for immediate investigation because of its important bearing on the problems of erosion, flood control, and water conservation, as

well as its relation to the successful establishment and maintenance of forest plantations on the farm and on waste land.

The work in this investigation covered both soil porosity and water-absorbing capacity. Because of contrasting conditions of forest and field soils, a comparison of these characteristics was made in four distinct phases, as follows: (1) Old-growth forest soil with open-field soil; (2) second-growth forest soil with open-field soil; (3) grazed with ungrazed second-growth forest soil; (4) forest-plantation soil with open-field soil.

SOIL POROSITY OF OLD-GROWTH FOREST AND OPEN FIELD

From among the very few forest stands in the Central States undisturbed by cutting, grazing, or recent fire, 22 areas were selected

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FIGURE 2.—Characteristic old-growth virgin soil

that were near enough to a natural condition to be suitable for the purposes desired. (Fig. 2.) These sites, in Ohio, Indiana, Michigan, and Illinois, were selected on the basis of no grazing, no cutting for at least 50 years except for the removal of an occasional tree, and no recent fire damage apparent. The absence of grazing was determined by the uniform distribution of age classes and by the available history of the woods. So far as could be determined from observation and checking with soil-survey data, the soils compared were of the same original type.

Twenty soil tests for apparent specific gravity, or air-dry weight divided by a constant volume, were taken on each area—10 in the forest and 10 in adjacent fields. This number varied in a few instances, but forest and field samples were paired on each site. Each

field site was selected as near the forest as possible as a precaution against variation in soil type between the two. The topography was observed and the samples taken as near the same elevation as possible. All surface litter and duff were removed from the forest soil in order that the comparisons might be made purely on the basis of mineral soil. The cultivated soil did not, of course, have the surface organic horizon. In addition to the 10 specific-gravity samples on each site, a 500-g sample was taken for moisture and real specific gravity determination. This latter sample was weighed immediately, placed in a pint cardboard box, and taken to the laboratory.

The apparent specific-gravity tests were made with the usual specific-gravity tube, a hollow iron cylinder 2½ inches in diameter and 12¼ inches long. One end was beveled on the outside to make a sharp cutting edge. This bevel, being on the outside, did not change the uniform inside diameter of the tube; hence, significant compression of soil did not result when the tube was driven in. With an iron plug turned from high-grade machine steel as a driving head and an 8-pound steel sledge, the tube was driven into the soil until only 3 inches projected above the surface, as determined by a groove machined around the tube. The core of soil 2½ inches in diameter and 9¼ inches long (6.35 by 23.5 cm with a volume of 744 cm^3) was removed from the tube and weighed.

TABLE 1.—*Average weights of constant soil volumes (744 cm^3) to a depth of 9.25 inches compared in various old-growth forest areas and adjacent open fields* [a]

Forest soil location	Forest soil	Open area	
		Description	Soil sample
	Grams		*Grams*
Keffer Woods, Mifflin, Ohio	[b] 945.6	Wheat stubble	[b] 1,087.1
State Sanatorium Woods, Mount Vernon, Ohio	912.8		1,061.2
Myers Woods, Oldenburg, Ind	956.2		1,053.0
Berkey Woods, Warsaw, Ind	1,155.7		1,244.4
Rosebrook Woods, Warsaw, Ind	1,010.4		1,078.2
Pines Park Woods, Dixon, Ill	970.2		1,114.4
Bent Tree Woods, Elizabeth, Ill	859.0		999.1
Foley's Woods, Paris, Ill	857.4		1,133.1
Rhymer Woods, Dongola, Ill	857.1		1,082.7
Turkey Run, No. 1, Marshall, Ind	[c] 879.1	Clover field	[d] 1,058.0
Turkey Run, No. 2, Marshall, Ind	[d] 900.5		1,058.0
Dillon Woods, Porter, Ind	928.2	Cornfield	1,013.2
Spring Mill Park, Mitchell, Ind	905.7		1,019.7
Lewis Woods, Williamsburg, Ind	860.5		1,079.5
Purdue University Woods, Farmland, Ind	916.1		1,042.0
Brownfield Woods, Urbana, Ill	914.3		1,134.4
Fricke Woods, Jonesboro, Ill	[e] 996.7		[e] 1,124.0
Reynolds Woods, Coruna, Ind	1,000.7	Pasture	1,147.4
Ellsworth Woods, Ellsworth, Ill	994.1		1,059.7
Liepold Woods, Mount Carmel, Ill	898.0	Cowpeas	1,018.2
Shades, Shades, Ind	1,019.1	(f)	----
Real or weighted average	[g] 936±3.2	----	[g] 1,079±2.6
Standard deviation	93.62	----	75.77

[a] 10 determinations unless otherwise noted.
[b] 20 determinations.
[c] 13 determinations.
[d] 12 determinations.
[e] Not included in average, as explained in text.
[f] No comparable field.
[g] Based on all determinations.

When the weights of this constant volume of different soils were tabulated and averaged (Table 1), it was found that the difference between average weights of forest and field soils was 143 g. In other words, the average field soil was 15.3 per cent heavier than the average

forest soil in the upper 9 inches. Since the samples were taken in August and September during an extremely dry period, moisture content was at a minimum in all samples included. Laboratory determinations show slightly higher percentages of moisture in woods than in field soils; therefore, the comparison of woods with field soil is justified on field-weight basis since the difference is slight and would tend to reduce rather than increase any difference between weights.

The Fricke Woods samples, which were not included in the average in Table 1, were the one exception in moisture content. These samples were taken at the end of the summer season after a sudden heavy rain. It is interesting to observe that when the samples were taken on the day following the rain, moisture had penetrated to a depth of 9 inches in the woods, on a 10 per cent slope, whereas in an adjoining field with less slope the penetration of moisture was only 3 inches. The difference was due undoubtedly to superficial run-off in the open. This belief is strengthened by observations of serious erosion damage in the field.

TABLE 2.—*Moisture, specific gravity, and pore space in old-growth forest and field soils*

Soil-sampling site	Capillary water		Hygroscopic water		Apparent specific gravity	
	Forest	Field	Forest	Field	Forest	Field
	Per cent	*Per cent*	*Per cent*	*Per cent*		
Myers Woods, Oldenburg, Ind	8.93	3.51	1.030	1.197	1.1801	1.3911
Berkey Woods, Warsaw, Ind	22.25	20.77	1.237	.962	1.2715	1.3857
Rosebrook Woods, Warsaw, Ind	22.25	15.74	1.565	1.172	1.1115	1.2526
Pines Park Woods, Dixon, Ill	17.64	13.12	1.520	1.817	1.1088	1.3252
Bent Tree Woods, Elizabeth, Ill	4.38	5.93	1.537	1.559	1.1061	1.2674
Foley's Woods, Paris, Ill	13.38	7.76	2.372	1.325	1.0175	1.4126
Rhymer Woods, Dongola, Ill	16.27	13.90	1.350	1.115	.9906	1.2782
Turkey Run, Marshall, Ind., No. 1	8.93	5.26	.759	1.262	1.0981	1.3508
Turkey Run, Marshall, Ind., No. 2	7.30	5.26	.840	1.262	1.1142	1.3508
Dillon Woods, Porter, Ind	13.63	13.89	.777	1.094	1.0887	1.1962
Spring Mill Park, Mitchell, Ind	7.99	13.38	1.245	2.825	1.1276	1.2903
Lewis Woods, Williamsburg, Ind	32.63	27.22	2.467	1.660	.8723	1.1424
Brownfield Woods, Urbana, Ill	14.94	8.93	2.290	1.310	1.0698	1.3992
Fricke Woods, Jonesboro, Ill	40.05	13.64	1.380	2.127	.9569	1.3306
Reynolds Woods, Coruna, Ind	13.63	10.86	1.450	1.612	1.1841	1.3925
Ellsworth Woods, Ellsworth, Ill	8.69	12.11	1.872	1.982	1.2298	1.2702
Liepold Woods, Mount Carmel, Ill	13.12	9.09	1.775	.972	1.0672	1.2594
Warren Woods, Three Oaks, Mich	6.16	1.83	.952	.645	1.1102	1.2298

Soil-sampling site	Real specific gravity		Pore space, with percentage excess in forest soil		
	Forest	Field	Forest	Field	Excess
			Per cent	*Per cent*	*Per cent*
Myers Woods, Oldenburg, Ind	2.598	2.618	54.57	46.86	16.45
Berkey Woods, Warsaw, Ind	2.585	2.611	50.81	46.93	8.27
Rosebrook Woods, Warsaw, Ind	2.584	2.517	56.98	50.23	13.44
Pines Park Woods, Dixon, Ill	2.607	2.598	57.47	48.99	17.31
Bent Tree Woods, Elizabeth, Ill	2.647	2.614	58.21	51.52	12.99
Foley's Woods, Paris, Ill	2.577	2.566	60.52	44.94	34.67
Rhymer Woods, Dongola, Ill	2.615	2.578	62.12	50.42	23.21
Turkey Run, Marshall, Ind., No. 1	2.620	2.619	58.08	48.42	19.95
Turkey Run, Marshall, Ind., No. 2	2.636	2.619	57.73	48.42	19.23
Dillon Woods, Porter, Ind	2.626	2.609	58.54	54.15	8.11
Spring Mill Park, Mitchell, Ind	2.615	2.703	56.88	52.26	8.84
Lewis Woods, Williamsburg, Ind	2.599	2.626	66.44	56.50	17.59
Brownfield Woods, Urbana, Ill	2.606	2.638	58.95	46.96	25.53
Fricke Woods, Jonesboro, Ill	2.649	2.706	63.87	50.83	25.65
Reynolds Woods, Coruna, Ind	2.608	2.642	54.60	47.29	15.46
Ellsworth Woods, Ellsworth, Ill	2.632	2.642	53.27	51.92	2.60
Liepold Woods, Mount Carmel, Ill	2.626	2.644	59.63	52.37	13.86
Warren Woods, Three Oaks, Mich	2.596	2.671	57.23	53.96	6.06

Table 2 shows the percentage of capillary water, the percentage of hygroscopic water, apparent specific gravity, real specific gravity, and percentage of pore space in forest and field soils, together with the percentage of excess pore space in forest over corresponding field soils.

Dry weights of field soils were calculated by multiplying the average of 10 field weights on each site by the moisture percentage determined on the 500-g sample taken for that site. The 500-g samples were air-dried and the capillary water calculated on the air-dry basis. The air-dry soil was oven-dried and the hygroscopic moisture determined on the oven-dry basis. Real specific gravity was determined by the usual pycnometer method. The volume of the core of soil in each case was 744 cm^3. Apparent specific gravity was determined by dividing the air-dry soil weight by 744.

Averages of real specific gravities for forest and field soils indicated only very slight differences—2.613 ± 0.0032 (standard deviation, 0.020) for forest soils and 2.623 ± 0.007 (standard deviation, 0.044)

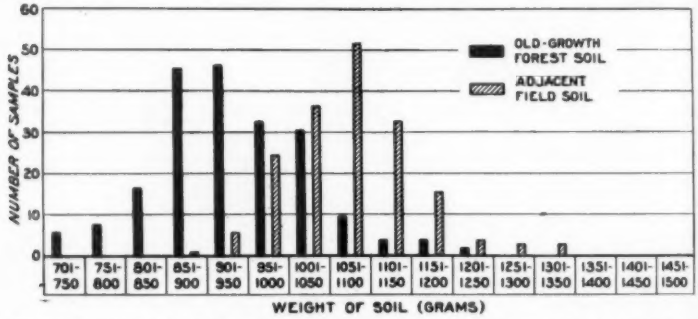

FIGURE 3.—Distribution of 405 samples (0-9.25-inch soil section) of old-growth forest and adjacent field soil

for field soils. The similarity of these figures eliminates serious question as to the possibility of the difference in forest and field soils being caused by difference in the actual weight of the soil material.

When the weights of the constant volume (744 cm^3) of soil are assembled into groups varying from 701 g to 1,350 g by class intervals of 50, as 701 to 750, 751 to 800, etc., a distinct difference in range of weights is exhibited in forest and field soils. This is shown in Figure 3.

The question naturally arises, to what depth does the increased porosity of forest soils extend? Does the difference occur only at the immediate surface or is it distributed throughout the entire 9-inch profile? This point is significant in the survival of tree seedlings, because if the increased porosity extends to any considerable depth, seedling roots will be able to penetrate much easier and the percentage of survival will be greater. The much mooted question as to difference in water-holding capacities of forested and cultivated areas would be clarified by knowledge of the extent of looseness below the surface.

To settle this question, specific-gravity tests were made the following year in each of three successive 3-inch soil sections in woods and

field on similar old-growth sites.[4] (Table 3.) By driving the 12¼-inch tube into the soil until lengths of 9, 6, and 3 inches remained above the soil surface, columns were obtained of 3.25, 6.25, and 9.25 inches, respectively. The second 3-inch column weight was obtained by subtracting the average weight for the 3.25-inch column in succession from each 6.25-inch column weight. Likewise, the weights of the third 3-inch column were obtained by subtracting the average weight of the 6.25-inch column from the 9.25-inch column weights. By this procedure, the weights obtained were for successive columns of 3.25, 3, and 3 inches.

TABLE 3.—*Average weights (grams) of constant soil volumes, on air-dry basis, at three different depths in various old-growth forest areas and in adjacent open fields* [a]

Forest soil location	Open areas	0–3.25 inch depth		3.25–6.25 inch depth		6.25–9.25 inch depth	
		Forest	Field	Forest	Field	Forest	Field
Morton Woods, Gallipolis, Ohio.	Pasture	251.5	397.1	316.8	316.7	307.3	371.7
Carnahan Woods, Oakwood, Ohio.	Pasture	191.3	339.1	282.5	364.6	276.3	240.9
Reynolds Woods, Coruna, Ind.	Pasture	251.3	372.8	251.3	345.5	417.6	337.4
Bent Tree Woods, Elizabeth, Ill.	Pasture	287.8	364.1	264.6	286.4	298.0	352.1
Sherman Grooms Woods, West Union, Ohio.	Meadow	296.6	386.9	309.9	292.9	------	------
Beech-maple Woods, Turkey Run, Ind.	Meadow	241.6	382.4	227.2	373.0	421.1	[b] 240.0
Ferris Woods, Fort Ancient, Ohio.	Cornfield	309.6	382.1	300.0	272.0	344.3	360.8
Dale Robinson Woods, Bethel, Ohio.	Cornfield	300.0	385.4	335.6	324.9	325.6	331.4
Snyder Woods, Forestville, Ohio.	Wheat field	241.6	381.1	339.7	357.7	274.0	303.1
Houston Woods, Oxford, Ohio.	Wheat field	340.9	398.5	319.4	318.5	270.0	362.5
Pines Park Woods, Dixon, Ill.	Wheat field	244.4	369.1	273.0	309.0	452.2	416.4
Brownfield Woods, Urbana, Ill.	Wheat field	255.2	400.2	285.0	381.6	394.3	350.4
Rhymer Woods, Dongola, Ill.	Wheat field	226.8	373.2	238.6	308.3	393.1	406.7
Dillon Woods, Porter, Ind.	Wheat field	225.8	347.2	297.9	296.8	404.2	369.6
Myers Woods, Oldenburg, Ind.	Wheat field	268.9	348.9	359.9	392.0	327.2	303.0
Real or weighted average		262±2.11	375±1.0	293±2.0	329±2.0	350	345
Standard deviation [c]		49.75	29.36	63.59	47.5	------	------

[a] Soil volumes were 241.3 cm³ at middle and lowest depths and 261.4 cm³ at first horizon. Values are averages of 10 determinations unless otherwise stated.
[b] Average 5 determinations.
[c] Based on all determinations.

The average weights of samples of the surface 3.25 inches were 262 g for forest-soil and 375 g for field-soil samples. This is a difference of 113 g or 43.13 per cent; in other words, the first 3.25 inches of an average field-soil area is on an average, 43.13 per cent heavier than the first 3.25 inches of an adjacent old-growth forest soil. This difference is based on the mineral soil below the litter and duff accumulation. Similarly, the average weight of the 3.25–6.25 inch soil section is 12.29 per cent greater for the field than for the woods soil. Figures 4 and 5 show the range and distribution of weights of the two lower soil sections. In the lowest section the difference is negligible, and

[4] The original soil weights of the first year's work are given on a field-weight basis, whereas the weights of the second year's work were on an air-dry basis. This will not alter the comparative relationship between forest and field soils, but should be taken into consideration if the actual weights of the first year's work are compared with those obtained the second year.

therefore no attempt was made to show graphically the distribution of weight classes.

From the foregoing comparisons it may be seen that the greatest difference in porosity between old-growth woods soil and cultivated soil is in the first 6-inches. But although the lower section shows no difference by apparent specific gravity measurements, water-absorp-

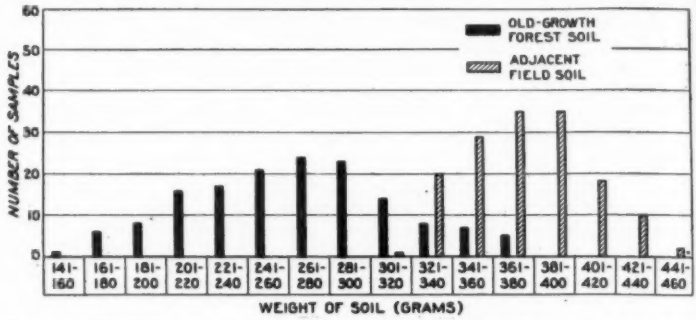

FIGURE 4.—Distribution of 300 samples (0–3.25 inch soil section) of old-growth forest and adjacent field soils, by weight classes

tion experiments show that the lower section at a depth of 8 inches absorbs water much more rapidly in woods than in field soil.

WATER ABSORPTION IN OLD-GROWTH FOREST SOILS

As a corollary to the measurements of apparent specific gravity, a series of absorption tests were made on virgin forest-soil areas and adjacent fields. Five brass tubes 2 by 12 inches were used. The tubes were sharpened on one end and forced into the soil to a con-

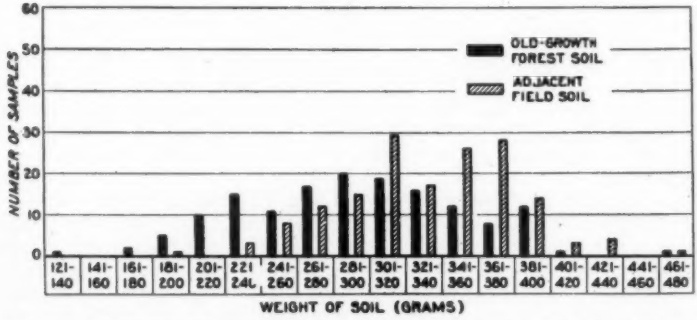

FIGURE 5.—Distribution of 300 samples (3.25–6.25 inch soil section) of old-growth forest and adjacent field soils, by weight classes

stant depth of 3 cm. This depth proved sufficient to insure that the water would not flow up around the end.

Absorption was measured at three different depths; 1, 3, and 8 inches. In the first depth, the litter or duff layer was removed. In the second or 3-inch depth, a trench 2 inches deep was dug before the tubes were driven in. In the lower depth, a trench 7 inches deep was

dug. This procedure placed the bottoms of the brass tubes 1, 3, and 8 inches below the soil surface.

The three tubes were kept filled to the top by means of five graduated cylinders each containing 800 cm³. At the end of 10 minutes the water remaining in each graduate was measured. This volume in each case added to the known constant volume of the corresponding brass tube, less the volume of the small column of soil at the bottom of the brass tube, and subtracted from 800, gave the amount absorbed. In the case of very rapid absorption, a smaller unit of time was used; and in the case of very slow absorption, the small amount of water was determined by measuring the level to which the water sank during the time interval, and by claculating its volume from the known diameter of the brass tube.

TABLE 4.—*Rates of water absorption in old-growth and open-field soils, in cubic centimeters per minute, at 1-inch, 3-inch, and 8-inch depths* [a]

Forest soil location	Open area	1-inch depth		3-inch depth		8-inch depth	
		Forest	Field	Forest	Field	Forest	Field
		Cc	Cc	Cc	Cc	Cc	Cc
Morton Woods, Gallipolis, Ohio	Pasture	165.8	0.8	6.0	1.2	1	1
Houston Woods, Oxford, Ohio	Pasture	11.0	1.2	1.2	1.4	2.4	5.2
Reynolds Woods, Coruna, Ind	Pasture	89.6	5.0	18.4	12.6	8.6	5.8
Bent Tree Woods, Elizabeth, Ill	Pasture	370.6	3.4	10.6	3.0	1.4	5.8
Sherman Grooms Woods, West Union, Ohio.	Cornfield	187.8	2.0	11.0	9.0	2.0	1.2
Ferris Woods, Fort Ancient, Ohio	Cornfield	12.0	1.2	4.0	1.4	.8	2.2
State Sanitarium Woods, Mount Vernon, Ohio.	Cornfield	60.2	5.2	21.8	2.4	12.2	3.2
Poplar Cove Woods, Haverhill, Ohio	Wheat stubble	144.0	3.6	10.8	4.6	1.2	2.0
Dale Robinson Woods, Bethel, Ohio	Wheat stubble	105.6	.6	8.0	5.6	1.4	.4
Snyder Woods, Forestville, Ohio	Wheat stubble	425.8	4.0	6.0	3.4	3.8	7.4
Pines Park, Dixon, Ill	Wheat stubble	822.4	4.6	24.2	2.4	5.6	3.0
Brownfield Woods, Urbana, Ill	Wheat stubble	175.4	4.6	139.8	3.0	4.8	2.4
Rhymer Woods, Dongola, Ill	Wheat stubble	282.8	1.8	446.2	5.8	15.0	2.4
Dillon Woods, Porter, Ind	Wheat stubble	423.8	5.8	236.0	4.8	5.6	4.4
Myers Woods, Oldenburg, Ind	Wheat stubble	175.6	2.6	92.8	7.6	2.2	.6
Daniel Mosier Woods, Spellacy, Ohio	Wheat stubble	127.6	11.0			27.6	7.8
Beech-maple Woods, Turkey Run, Marshall, Ind.	Meadow	194.8	9.8	113.8	9.2	14.4	9.4
Keffer Woods, Mifflin, Ohio	Meadow	84.6	4.6			50.2	3.4
Chas. Armstrong Woods, Loudonville, Ohio.	Meadow	32.6	3.8			15.0	5.4
Average (rounded)		205	4	72	5	9	4

[a] Each figure represents the average of 5 determinations.

Table 4 shows the average absorption per minute at the three depths in woods and field. The ratios of water absorption per minute at the 1, 3, and 8 inch depths in forest and field were 205 to 4, 72 to 5, and 9 to 4, respectively.

This method of measuring absorption rates must be considered only relative. Rainfall water penetrates only vertically downward, the water of adjacent areas prevents the horizontal movement possible from the tubes. Horizontal absorption is, however, roughly proportional to porosity; consequently, on a comparative basis, the procedure is justifiable. The relative rates of absorption in forest and field strengthen the conclusion drawn from the apparent specific gravity measurements, namely, that forest soils are more porous than field soils. (Fig. 4.)

On 36 second-growth areas in Ohio, representing nearly all major soil areas of the State, 718 specific-gravity tests were made in the

0–9.25 inch horizon. (Table 5.) The average weight of 744 cm^3 of dry soil was, for the second-growth woods, 873 g and for the adjacent field soil 1,023 g. Figure 6 shows the distribution of weight classes as between the forest and open soils. The significant fact about this comparison is that the second-growth woods soil is much more porous than the corresponding field soil. Apparently any deleterious effect of the cutting on soil tilth has been remedied by the closing in of the crowns and the prompt reestablishment of a litter cover.

TABLE 5.—*Average weights of constant soil volumes (744 cm^3) to a depth of 9.25 inches of ungrazed second-growth forest areas and adjacent open fields or heavily grazed woods [a] in Ohio*

Forest-soil location	Ungrazed forest soil	Open or grazed area	
		Soil sample	Description
	Grams	*Grams*	
Richmondale	935.1	1,062.2	Abandoned field.
Athens	[b] 947.1	1,002.2	
Idaho	880.7	1,016.6	
Indian Springs	850.5	1,015.3	Meadow.
Bentonville	881.6	1,033.2	
Russellville	945.4	1,050.5	
Meeker	[b] 817.2	1,044.7	
Brighton	1,003.4	1,128.2	
Mutual	1,000.4	1,159.5	
Columbus	971.5	1,032.3	
Johnsville	872.9	1,039.3	
Vermilion	739.8	936.4	
West Union	944.5	947.0	Pasture.
Bethel	898.1	1,092.1	
Batavia	928.4	1,008.5	
Montgomery	836.5	1,045.7	
Circleville	833.4	1,067.4	
Do	935.2	1,108.2	
Marion	918.7	1,164.2	
Mansfield	769.7	1,043.1	
Mount Vernon	824.3	999.1	
Sunbury	895.1	975.2	
Marysville	910.8	998.5	
Alta	766.2	1,024.9	
Clyde	885.0	1,134.7	
Bucyrus	803.0	993.6	Heavily grazed woods.
Marengo	853.9	996.8	
Clarksville	931.3	950.6	
Marion	832.2	946.5	Typical examples of grazed and ungrazed woods. [c]
Upper Sandusky	837.9	969.1	
Marion	906.6	993.9	
Galion	679.7	837.8	
Mansfield	827.1	1,038.7	
Lexington	874.6	915.1	
Mount Gilead	882.7	1,043.1	
Mount Vernon	810.8	1,030.5	
Real or weighted average [c]	873±2.5	1,023±2.4	
Standard deviation [d]	97.9	81.1	

[a] Averages of 10 determinations unless otherwise noted.
[b] Average of 9 determinations.
[c] Average of 9 typical examples, ungrazed woods, 843±4.9 g (S. D. 68.7), grazed woods, 969±4.5 (S. D. 63.0).
[d] Based on all determinations.

Where grazing has been practiced, soil porosity has been much reduced. Apparently conservative cutting in this region preserves soil porosity. Even where cutting has been severe, the reestablishing of a litter cover has prevented excessive soil deterioration. This fact is at once apparent when a comparison is made between the differences in weights of old-growth forest soil and adjacent field soils, and the differences between second-growth woods soil and adjacent field soil. They are 144 and 150 g, respectively, for the 9.25-inch column 2½ inches in diameter. This demonstrates that soil porosity is main-

tained in second-growth woods soil. This general conclusion is strengthened when it is appreciated that the sites were selected at random and represented oak-hickory, beech-maple, pure beech, pure oak, mixed mesophytic, and elm-ash-maple forest types. The soils of the various sites represented glaciated and unglaciated areas, limestone and sandstone understrata, Wisconsin and Illinoian glaciation, flat and rolling topography, well drained and poorly drained sites. The second-growth woods in every case showed a lighter soil than did the field areas adjacent. The second-growth woods were of all ages from 10 to 70 years. Cutting had been severe in many instances, but in practically all cases the crown cover had filled in the vacant spaces.

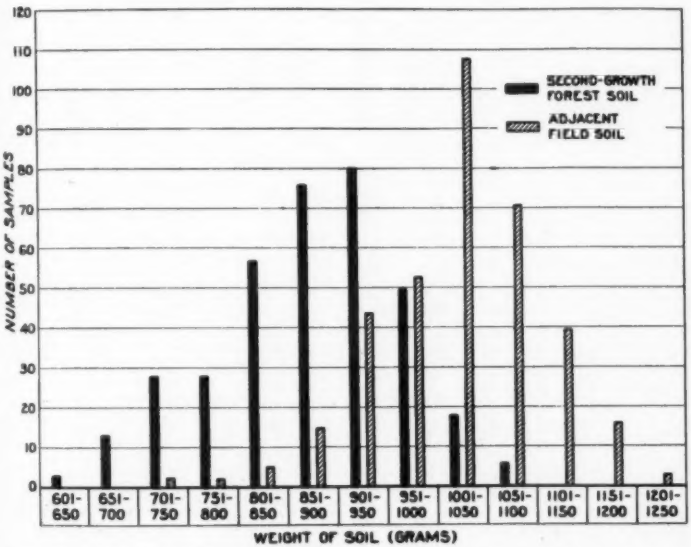

FIGURE 6.—Distribution of 718 samples (0–9.25 inch soil section) of second-growth forest and adjacent field soils, by weight classes

SOIL POROSITY OF GRAZED AND UNGRAZED WOODS

From the list of second-growth sites, nine were selected as typical of grazed and ungrazed woods. The grazed woods were in the last stages of forest degradation—that is, there were only a few old trees, no reproduction, and a ground cover of weeds, grass, and sod. Table 5 gives the weights of the 0–9.25 inch soil section. Figure 7 presents a comparison of grazed and ungrazed areas, as shown in the distribution of weight classes. The average weight of the 744 cm^3 core of soil on the basis of 180 samples of air-dry soil was 843 g for the ungrazed, and 969 g for the grazed areas, a difference of 126 g. This, interpreted in percentages, means that a grazed woods soil in the 0–9.25 inch section is 15 per cent heavier than the corresponding soil section in an adjacent ungrazed area. Excessive grazing not only prevents tree reproduction but also makes forest exhaustion inevitable through compaction of the soil. The grazed soil is harder, holds less moisture, has poorer aeration, and its general tilth is much deteriorated.

SOIL POROSITY IN FOREST PLANTATIONS AND OPEN FIELDS

The final angle of the soil porosity question deals with forest plantation sites. Does soil porosity return to old fields after planting? Thirteen plantations were measured for soil porosity and compared to

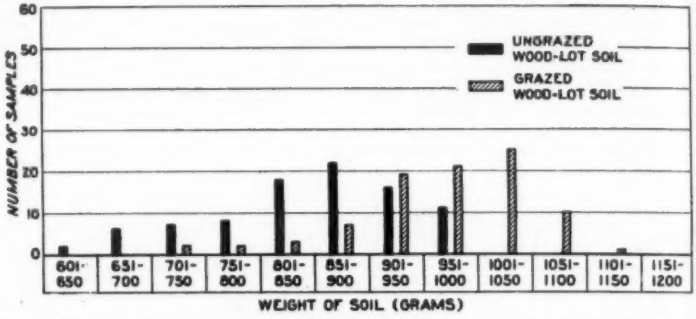

FIGURE 7.—Distribution of 180 samples (0–9.25 inch soil section) of grazed and ungrazed wood-lot soils, by weight classes

adjacent field sites. (Table 6.) The difference in average weight of 744 cm^3 cores of forest plantation soil and field soil was 128 g, or a 13.6 per cent greater weight for field soil than for adjacent plantation soil. Figure 8 shows the distribution of weight classes. The lighter

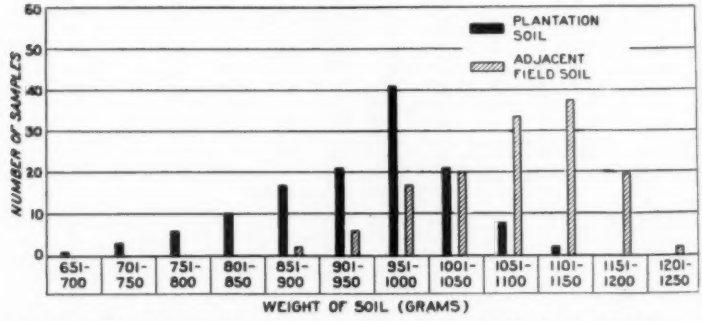

FIGURE 8.—Distribution of 259 samples of plantation and adjacent field soils, by weight classes

average for plantation soil represents a gain in porosity since planting. Field observations show that as soon as a litter is established under a stand the soil becomes more porous. The observation was made that the soil of conifer plantations gained more in porosity in a given time than did that of the hardwoods.

TABLE 6.—*Average weights [a] of constant volumes of soil (744 cm³) to a depth of 9.25 inches in forest plantations and adjacent open fields*

Location	Plantation			Open area	
	Species [b]	Age	Soil sample	Description	Soil sample
		Years	*Grams*		*Grams*
Fremont, Ohio	Hardy catalpa	29	1,006.0	Pasture	1,084.5
	Scotch pine and Norway spruce	19	927.4	do	1,081.4
	Northern white pine	20	950.8	do	1,081.4
Wooster, Ohio	Norway spruce	14	937.7	do	1,081.4
	Beech	15	993.1	do	1,081.4
	Norway pine and Norway spruce.	18	926.7	do	1,081.4
Colebrook, Ohio	do	15	792.2	Abandoned field	929.4
Athens, Ohio	Norway pine	12	980.3	Cornfield	1,033.9
	Corsican pine	12	1,065.5	do	1,093.5
Urbana, Ill	Bur oak	42	834.3	do	1,134.4
	European larch	59	982.3	do	1,134.4
Athens, Ohio	Northern white pine	23	972.7	Sod	[c] 1,088.4
Marietta, Ohio	Norway pine	17	886.3	do	1,021.4
Real or weighted average			943±5.1		1,071±4.2
Standard deviation			85.64		70.97

[a] Averages of 10 determinations unless otherwise noted.
[b] Botanical names of species are as follows: Hardy catalpa (*Catalpa speciosa* Ward); Scotch pine (*Pinus sylvestris* L.); Norway pine (*P. resinosa* Sol.); northern white pine (*P. strobus* L.); Corsican pine (*P. nigra* var. *poiretiana* Asch. and Graebn.); Norway spruce (*Picea abies* Karst.); European larch (*Larix decidua* Mill.); beech (*Fagus grandifolia* Ehrh.); bur oak (*Quercus macrocarpa* Mich.).
[c] Average of 9 determinations.

WATER ABSORPTION IN FOREST-PLANTATION SOIL

Water absorption tests in plantation and adjacent field soils demonstrated that plantation soils have a much greater absorption capacity. (Table 7.) The average for the plantation sites at the 1-inch depth was 107 cc per minute and for the field site at 1-inch depth, 8 cc. At the 8-inch depth, the averages were 13 and 3 cc per minute for the plantation and field sites respectively. These differences in absorption capacity justify the weight differences recorded and show a gain in soil porosity for the plantation since planting.

TABLE 7.—*Average rate of water absorption in cubic centimeters per minute in forest plantation and adjacent field soil* [a]

Location	Plantation				Open area		
	Species [b]	Age	Soil sample		Description	Soil sample	
			1-inch depth	8-inch depth		1-inch depth	8-inch depth
		Years	*Cc*	*Cc*		*Cc*	*Cc*
Wooster, Ohio	Scotch pine and Norway spruce.	19	32.6	4.6	Pasture	5.2	4.2
	Northern white pine.	20	21.0	14.6	do	5.2	4.2
	Beech	15	81.4	3.2	do	5.2	4.2
	Norway pine and Norway spruce.	18	69.8	3.4	do	5.2	4.2
Colebrook, Ohio	Norway spruce	15	367.4	1.0	Abandoned field	44.8	5.0
Athens, Ohio	Norway pine	12	8.6	2.4	Cornfield	4.4	1.2
	Corsican pine	12	5.6	6.2	do	4.4	2.8
Urbana, Ill	European larch	59	521.8	69.8	do	4.6	2.4
	Bur oak	42	42.4	30.4	do	4.6	2.4
Athens, Ohio	Northern white pine.	23	13.8	2.6	Sod	3.6	2.8
Marietta, Ohio	Norway pine	17	7.8	1.2	do	2.0	1.6
Average (rounded)			107	13		8	3

[a] Each value is the average of 5 determinations.
[b] For botanical names, see Table 6, footnote *b*.

FUNCTIONS OF FOREST LITTER

The problem of forest soils is inseparably connected with forest litter, and the proper production and retention of adequate quantities and kinds of forest litter is inseparably connected with good silvicultural practice. This relationship of litter to good forestry methods may be appreciated better when the many functions of litter are considered. The accumulation of litter depends upon three major factors: Moisture, temperature, and ease of decomposition. Given a high average temperature and a sufficient supply of moisture, leaf litter decomposes very rapidly. In the Tropics, for instance, leaf litter does not accumulate to any great extent because of the high average temperature and high humidity. Indeed, the oxidation is so rapid that not only does the leaf litter disappear, but the soil itself is oxidized to a considerable depth, a condition which gives rise to the so-called laterite or red soil. In the Temperate Zone the accumulation of leaf litter is more rapid and in the sub-Arctic Zone the accumulation of litter becomes so great that it may actually be a deterrent to tree growth. It locks up the plant food in the rather tight layer of raw vegetative material, the rate of decay of which is not rapid enough to return plant food to the soil.

In the Central States region the accumulation of litter small compared with that in the northern spruce belt. In fact, it is seldom more than 1 inch deep. The leaf fall decomposes rapidly and adds its fertility to the soil. The forest litter is, however, of great importance in this region even though it does not accumulate to a great depth. It serves as an absorbent, acts as a mulch or insulation against rapid evaporation, prevents compaction of surface soil by impact of rain, decomposes and furnishes plant food, and serves as a medium for microbiological activities.

Structure of forest soil has been developed through long periods of time. Root penetration, expansion, and contraction, with changes in temperature and moisture content, and activities of worms, insects, and animals, make soil porous. The forest with its protective soil cover of leaf litter and its deep root system is a builder and preserver of soil porosity. The penetration of roots and their eventual decay leave the soil interpenetrated with tubelike cavities. (Fig. 9.)

The process of cropping, on the other hand, ultimately decreases soil porosity and favors erosion. For example, the increased porosity brought about by freezing and thawing is preserved in forest soils by the covering of litter, but in field soils it is largely lost in summer by impact of rain and silting and alluviating action of percolating waters. When the Central States region was settled originally, both good and poor lands were cleared and cultivated. The accumulation of organic matter in the form of incorporated and unincorporated forest litter afforded a temporary supply of plant food, and even the poorer, shallow soils produced well for a generation. Then this supply became exhausted and the land ceased to pay a reasonable return for its cultivation. As the organic matter oxidized and plant food leached away, the soil became increasingly unproductive. The impoverishment under agricultural use of originally fertile forest soil became a major factor in the growth of land abandonment.

The following is quoted (*6, p. 4*) from a report of a recent economic survey of Vinton County, Ohio:

There are 263,680 acres of land in the county. In 1880 the area of land in farms was 230,000 acres; by 1910, this had declined to 216,000 acres, and by 1930, to 152,000 acres, or 58.8 per cent of the total land area. In 1930 the area of improved land in the county was less than one-half that in 1900, and the number of farms in the county has decreased from 2,089 in 1900 to 1,823 in 1910 and to 1,075 in 1930.

Such a record needs no interpretation; it speaks deforestation, abandonment, and erosion.

DISCUSSION AND CONCLUSIONS

Under virgin conditions an equilibrium has been reached—the kinds and quantities of litter added to the soil do not vary much from season to season and the rate of decomposition has reached a norm.

FIGURE 9.—Old-growth forest soil, showing spongelike appearance due to penetration and decay of roots

The tree species best fitted to produce on the site have become established; theoretically, optimum conditions exist for that site. When cutting is done, certain species are usually selected, and the litter equilibrium is thereby disturbed. More sunlight is admitted, the ground cover changes; but after a period of years the crown cover closes in and another equilibrium is established.

The porosity of old-growth forest soil in the upper 9 inches is from 10 to 20 per cent greater than that of adjacent cultivated soil. The difference may be as much as 30 per cent in certain areas. The difference is greatest in the first 3 inches, decreases in the second, and becomes small in the third 3 inches. The method used in this investigation had a rather great limit of error, and although the average weights of forest and field soil were found to be about the same in the

6.25- to 9.25-inch horizon, observation confirmed by absorption tests show that there is a difference in porosity even at a 9-inch depth. For example, forest soils at a depth of 8 inches absorbed water more than twice as fast as did field soils at the same depth.

Not only are old-growth forest soils porous, but many of those examined in this study were also found to be platy in structure. (Fig. 10.) A platy soil has greater water-holding capacity than one

FIGURE 10.—A platy forest soil 9-249804

with no structure or with vertical cleavage. Water flows out into the horizontal cleavage planes and is thereby held in the soil in greater quantity than it would be if it were free to flow downward through cracks.

The effects of greater soil porosity in the forested areas are immediately apparent. When one considers that absorption from tubes is over 50 times as fast in old-growth forest soil at 1-inch depth as in cultivated fields at the same depth, the relative amounts of run-off in the respective sites may be visualized. While it is true that there was horizontal absorption in the case of the tubes, it must also be observed that even with horizontal absorption the amount of water taken up in field soil was extremely low. In many cases only a few cubic centimeters were absorbed, whereas in the woods the water ran into the soil with great rapidity. From the standpoint of applying the data to actual rainfall, it is at once clear that there would usually be consid-

erable run-off from even a ½-inch precipitation in the field areas, whereas a forest soil would have no difficulty in absorbing such a rain. Even a sudden rain of an inch or more, which is unusual in this region, would ordinarily be absorbed in a dry forest soil.

Virgin forests, except as a valuable means of interpreting optimum growth conditions, are of no concern in the Central States region. The virgin woods are gone; only second-growth and abandoned fields remain. One point is clearly established in respect to second-growth woods and that is the retention of soil porosity. Careful cutting and consequent opening up of the stand does not destroy soil porosity, provided the forest cover is quickly reestablished. A comparison of the weights of soil columns from second-growth woods and fields with those from old-growth forests and fields proves this point. Where the litter has not been destroyed by fire or grazing, the second-growth woods soil retains its virgin porosity to a surprising degree. The crown cover, of course, closes in after cutting and the litter produced reaches an equilibrium again.

The retention of soil porosity in second-growth woods emphasizes the prime importance of fire protection. Given proper protection and good silvicultural management in the way of selective cutting, practically all of the second-growth areas will retain their productive capacity.

What has been said regarding fire protection applies with equal force to overgrazing. Grazing is very injurious to soil structure. Compaction accompanies grazing and compaction means smaller water-holding capacity, poorer aeration, and general decrease in tilth and productivity. Trees become stag-headed where grazing is continued, litter largely disappears, sod forms, and the woods grow thin and finally disappear. Moderate cutting alone does not destroy soil porosity. The study of second-growth areas establishes the fact that soil porosity of old-growth areas is largely retained in second-growth woods provided grazing has not been practiced.

A problem of great concern in this Central States region is that of abandoned land and soil erosion. Six and a half million acres of land are considered idle. Most of this area was once wooded; now its fertility is largely exhausted by cultivation and erosion. The rule in the past has been to plant on such lands the species which formerly grew there naturally or to trust to luck that the area would become reseeded, without realizing that the cleared and abandoned field soil might not be capable, in its condition of deterioration, of favoring the reestablishment of the original tree growth. Some difficulty has been experienced in getting hardwood plantations established on such lands; conifer plantations, especially of pine, are as a rule more successful. Hardwoods, with the exception of black locust, are not so able to survive extremes of temperature and moisture deficiency, such as often occur in worn-out soil.

Conifers offer a means of bridging over the unfavorable period between abandonment and reforestation. On some lands planting is necessary to develop a cover. Before initiating a planting program, however, it is well to observe the condition of the soil. If the soil lacks structure, bakes badly, and is subject to severe drying in summer, hardwoods will probably fail. Many denuded areas will reseed eventually and regenerate naturally where there are seed trees. Such abandoned areas gradually seed in and establish a stand; then,

as a litter cover develops, the soil improves and severe extremes of temperature and moisture are obviated, paving the way for hardwoods. Such a transition is, however, often very slow.

In brief, from the results obtained in the studies here detailed, the following conclusions may be drawn:

Forest soil is much more porous than field soil.

Forest soil porosity is greatest in the upper 6 inches.

Porosity differences in forest soil and field soil are caused more by soil structure than by organic matter content, as shown by real specific gravity measurements.

Forest soil absorbs water much more rapidly than does field soil.

Water absorption is most rapid in forest soil at 1-inch depth and gradually decreases downward.

Ability of bare soil to absorb water is less at the surface than at 3-inch depth. A crust forms on the surface from impact of rain.

Where the forest cover is adequately maintained, second-growth forest soil does not lose its porosity unless grazing has been practiced to excess or the litter has been destroyed by fire.

Forest soil shows great loss of porosity when overgrazed.

Plantations on cultivated fields regain a large degree of soil porosity in 20 to 25 years as evidenced by soil weight and ability to absorb water.

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INHERITANCE OF FUSARIUM RESISTANCE IN BRUSSELS SPROUTS AND KOHLRABI [1]

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INTRODUCTION

The inheritance of resistance in both wild and cultivated cabbage (*Brassica oleracea* L. and *B. oleracea capitata* L.) to the yellows disease caused by *Fusarium conglutinans* Woll. was found by Walker [2] to be based upon a single dominant Mendelian factor. Moreover, it has been pointed out by Walker and Wellman [3] that the subspecies of *B. oleracea* other than cabbage are also susceptible to the yellows organism and that considerable differences in percentages of susceptible individuals are found among the commercial varieties of any one of the subspecies. The present paper is the report of a study of the inheritance of resistance to yellows in two of the subspecies of *B. oleracea*, namely, Brussels sprouts (*B. oleracea gemmifera* DC.) and kohlrabi (*B. oleracea caulo-rapa* DC.).

METHODS

The methods employed in this study were similar to those reported in the studies on cabbage.[4] Initial selections of resistant material were made from commercial varieties of Brussels sprouts and kohlrabi which had been grown on soil heavily infested with yellows. The selected material was brought to flower in the greenhouse, where controlled pollination was practiced.

Field trials were conducted in Kenosha County, Wis., on soil which was known to be thoroughly infested with the yellows organism. Seed was planted in seed beds and the resulting seedlings were transplanted to the trial plot. As symptoms of the disease appeared, with the advent of favorable soil temperatures, the diseased plants were permanently marked by means of bamboo stakes. Greenhouse trials of many of the plant progenies were conducted under controlled conditions of soil temperature in soil into which the yellows organism had been previously introduced. In the results as presented no distinction has been made in regard to the severity of the infection. Plants classified as diseased include those that showed any degree of yellows infection, ranging from symptoms so slight as to permit eventual recovery to those so severe as to cause the death of the plant. The delayed attack of the organism or its mild pathogenicity in some plants as contrasted with very severe forms of the disease in other

[1] Received for publication Nov. 22, 1932; issued July 1933. Cooperative investigations between the Division of Horticultural Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Department of Plant Pathology, University of Wisconsin.

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plants, can not be fully explained. As stated elsewhere,[5] these differences may depend on factors as yet unrecognized.

EXPERIMENTAL RESULTS

Commercial lots of Long Island Improved Brussels sprouts and White Vienna kohlrabi were grown on the yellows plot for three successive years. The results given in Table 1 show that the percentage of resistant plants was much higher in each of these varieties than in a commercial susceptible cabbage variety grown for comparison. Selections of Brussels sprouts and kohlrabi were made from plants that remained free from the yellows disease throughout the season of 1928. After the customary period in storage the plants were brought to the greenhouse and came to flower during the following winter. The data on inheritance of Fusarium resistance in each of the two subspecies will be considered separately.

TABLE 1.—*Occurrence of yellows in field trials of commercial varieties of Brussels sprouts, kohlrabi, and cabbage*

Common name and variety	Year	Plants grown on yellows plot			
		Total	Healthy	Diseased	
		Number	*Number*	*Number*	*Per cent*
Brussels sprouts, Long Island Improved	1928	76	67	9	12
	1929	40	31	9	23
	1930	104	80	24	23
Total		220	178	42	19
Kohlrabi, White Vienna	1928	75	46	29	39
	1929	50	40	10	20
	1930	84	71	13	15
Total		209	157	52	25
Cabbage, Danish Ballhead	1928	549	10	539	98
	1929	1,095	62	1,033	94
	1930	1,277	52	1,225	96
Total		2,921	124	2,797	96

INHERITANCE OF RESISTANCE IN BRUSSELS SPROUTS

Of the Brussels sprouts plants selected in the field, three (BS–3, BS–4, BS–6) were brought to flower in the greenhouse, and progenies from self-pollination were tested in the field and in the greenhouse in 1929. The results show (Table 2) that plant BS–3 was homozygous for resistance, whereas the progenies from BS–4 and BS–6 segregated into resistant and susceptible classes in a ratio approximating 3 resistant to 1 susceptible. These data indicate that resistance was inherited in a manner similar to that noted for cabbage.[5]

[5] WALKER, J. C. Op. cit. (See footnote 2.)

TABLE 2.—*Occurrence of yellows in progenies from self-pollination of three resistant Brussels sprouts plants selected from a commercial strain of Long Island Improved variety, 1929*

Genotype class	Progeny No.	Tested in—	Number of plants		Deviation	Probable error	Dev. / P. E.
			Healthy	Diseased			
RR	BS–3s	Field	21	0	0		
		Greenhouse	33	0	0		
Total			54	0	0		
Rr	BS–4s	Field	12	5	.75	±1.20	0.62
		Greenhouse	13	3	1.00	±1.17	.85
	BS–6s	Field	9	3	0	±1.01	0
		Greenhouse	13	14	7.25	±1.52	4.77
Total			47	25	7.00	±2.48	2.82
Calculated (3:1).			54	18			

Plants BS–3 and BS–4 were also crossed with a plant (C–131) from a line of Copenhagen Market cabbage which had previously been found to be homozygous for susceptibility. As a test of susceptibility, seed from self-pollination of plant C–131 was planted in the yellows plot. Of the 20 plants tested, all succumbed to yellows. The results of trials in 1929 with crosses between Brussels sprouts and cabbage are given in Table 3. That BS–3 was a homozygous resistant plant was confirmed by the fact that the hybrid progeny was completely resistant. On the other hand, the hybrid progeny from the supposedly heterozygous plant (BS–4) segregated in a ratio approximating 1 resistant to 1 susceptible.

TABLE 3.—*Occurrence of yellows in hybrid progenies from crosses between a homozygous susceptible cabbage plant (C–131) and two resistant Brussels sprouts plants, one (BS–3) homozygous for resistance, the other (BS–4) heterozygous for resistance, 1929*

Cross	Tested in—	Number of plants		Deviation	Probable error	Dev. / P. E.
		Healthy	Diseased			
BS–3 × C–131	Field	21	0	0		
	Greenhouse	25	0	0		
Total		46	0	0		
BS–4 × C–131	Field	14	15	.50	±1.82	0.27
	Greenhouse	9	21	6.00	±1.85	3.24
Total		23	36	6.50	±2.59	2.51
Calculated (1:1)		29.5	29.5			

From the field trials of the F_1 hybrids in 1929, material was saved from BS–3 × C–131 (*RR* × *rr*) and brought into the greenhouse. These plants, all of which were expected to be heterozygous (*Rr*) for resistance, were given numbers (BC–2, BC–3, etc.). Self-pollination was practiced on these plants, as well as emasculation and back crossing with plants from a homozygous susceptible cabbage line of Smith Pride variety (SP–5 and SP–9). Table 4 shows the reaction to the yellows organism, in the field and in the greenhouse, of the F_2 progenies resulting from self-pollination of the F_1 hybrid plants. In the field

trials segregation was very close to the expected ratio of 3 resistant to 1 susceptible. In the greenhouse trials the number in the susceptible class was appreciably below that expected, probably because of the failure of the soil temperature to maintain a level sufficiently high for disease expression, as discussed in a paper by Walker and Smith.[6]

TABLE 4.—*Occurrence of yellows in F_2 progenies from a cross between a homozygous resistant Brussels sprouts plant (BS–3) and a homozygous susceptible cabbage plant (C–131)*

Progeny No.	Tested in—	Number of plants		Deviation	Probable error	Dev. / P. E.
		Healthy	Diseased			
BC–2s	Field	59	14	4.25	±2.50	1.70
	do.[a]	30	10	0	±1.85	0
	Greenhouse	176	48	8.00	±4.37	1.83
BC–4s	Field	24	11	2.25	±1.73	1.30
	Greenhouse	31	8	1.75	±1.82	.96
BC–5s	Field	26	9	.25	±1.73	.14
	Greenhouse	93	16	11.25	±3.05	3.69
BC–6s	Field	9	2	.75	±.97	.77
BC–8s	Field	27	8	.75	±1.73	.43
	Greenhouse	126	34	6.00	±3.69	1.63
BC–9s	Field	14	6	1.00	±1.31	.76
BC–10s	Field	24	8	0	±1.65	0
	Greenhouse	12	4	0	±1.17	0
BC–11s	Field	5	3	1.00		
Total in field		218	71	1.25	±4.97	.25
Total in greenhouse		438	110	27.00	±6.84	3.95
Grand total		656	181	28.25	±8.45	3.34
Calculated (3:1)		628	209			

[a] Test made in 1931; other tests were made in 1930.

The progenies from back crosses between the F_1 hybrid plants and homozygous susceptible cabbage were also tested in the field and in the greenhouse. The field tests include trials made in 1930 and in 1931. As indicated in Table 5, the number of diseased plants in the field trials was considerably smaller than the number expected. This discrepancy may be explained, partly at least, by the fact that the seed bed in 1930 was inadvertently made on soil in which the yellows organism was present. Consequently, part of the susceptible class was eliminated in the seed bed and fewer individuals of that class were transplanted and considered in the field trial. In view of this possible explanation for the unusually small number of individuals in the susceptible class, certain progenies (BC–3 × SP–5, BC–4 × SP–5, and BC–11 × SP–9) were tested in the field the following year. The segregation in the second field trial of these progenies was in general closer to the expected 1 to 1 ratio. In 1930 the three progenies showed 96 healthy and 46 diseased plants, whereas in 1931 the same progenies showed 147 healthy and 134 diseased. Moreover, in greenhouse trials during the winter of 1930, as in 1931 field trials, the progenies segregated into healthy and diseased classes in a ratio reasonably close to the expected 1 to 1. The total of all trials shows a deviation which might be significant were it not for the explanation already given; in view of the normal behavior of these progenies in the greenhouse trial and in the second field trial, however, the large total deviation is not considered significant.

[6] WALKER, J. C., and SMITH, R. EFFECT OF ENVIRONMENTAL FACTORS UPON THE RESISTANCE OF CABBAGE TO YELLOWS. Jour. Agr. Research 41: 1–15, illus. 1930.

TABLE 5.—*Occurrence of yellows in progenies resulting from back crosses between F_1 hybrid plants (Rr) (from cross BS–3 (RR) × C–131 (rr)) and plants of a homozygous susceptible cabbage line (SP), 1930 and 1931*

Cross	Tested in—	Number of plants		Deviation	Probable error	Dev. / P. E.
		Healthy	Diseased			
BC–2 × SP–5	Field	48	29	9.50	±2.96	3.21
	Greenhouse	14	14	0	±1.78	0
BC–3 × SP–5	Field	46	20	13.00	±2.74	4.75
	do.[a]	28	28	0	±2.52	0
BC–4 × SP–5	Field	42	22	10.00	±2.70	3.70
	do.[a]	91	96	2.50	±4.61	.54
	Greenhouse	124	121	1.50	±5.28	.28
BC–5 × SP–5	Field	36	23	6.50	±2.59	2.51
	Greenhouse	255	241	7.00	±7.51	.93
BC–6 × SP–5	Field	36	19	8.50	±2.50	3.40
	Greenhouse	34	26	4.00	±2.61	1.53
BC–8 × SP–5	Field	26	27	.50	±2.46	.20
	Greenhouse	70	55	7.50	±3.77	1.99
BC–9 × SP–5	Field	33	20	6.50	±2.46	2.64
	Greenhouse	100	105	2.50	±4.83	.52
BC–10 × SP–9	Field	29	12	8.50	±2.16	3.94
	Greenhouse	56	68	6.00	±3.76	1.60
BC–11 × SP–9	Field	8	4	2.00	±1.17	1.71
	do.[a]	28	10	9.00	±2.08	4.33
Total in field		451	310	70.50	±9.30	7.58
Total in greenhouse		653	630	11.50	±12.08	.95
Grand total		1,104	940	82.00	±15.25	5.38
Calculated (1:1)		1,022	1,022			

[a] Test made in 1931; other tests were made in 1930.

INHERITANCE OF RESISTANCE IN KOHLRABI

Four kohlrabi plants (Kr–2, Kr–3, Kr–4, and Kr–6), selected in the field from the commercial stock, were brought to flower in the greenhouse. Progenies were tested in the field and in the greenhouse in 1929. As shown in Table 6, the progeny of Kr–2 segregated into healthy and diseased classes in approximately a 3 to 1 ratio, although the numbers involved were too low to make this result significant. Kr–3, Kr–4, and Kr–6 appeared to be homozygous for resistance. Certain sib crosses were made involving plants Kr–2, Kr–3, and Kr–4. Trials of the progenies from these crosses showed no yellows, a further indication that Kr–3 and Kr–4 were homozygous for resistance. Moreover, a cross between Kr–3 and susceptible cabbage C–131 yielded a completely resistant progeny. Three plants from the selfed progeny of Kr–3 were grown to seed the following winter. All three were self-pollinated and two were back crossed to susceptible cabbage. All progenies from self-pollination and from back crosses were completely resistant.

TABLE 6.—*Occurrence of yellows in progenies from four resistant kohlrabi plants selected from a commercial strain of White Vienna variety, 1929*

Progeny from—	Parent plant or cross No.	Tested in—	Number of plants		Genotype class of parent plants
			Healthy	Diseased	
Self-pollination	Kr–3	Field	27	0	*RR.*
		Greenhouse	29	0	*RR.*
	Kr–4	Field	27	0	*RR.*
		Greenhouse	31	0	*RR.*
	Kr–6	Field	12	0	*RR.*
	Kr–2	do	10	4	*Rr.*
Sib crosses	Kr–3 × 2	do	28	0	*RR* × *Rr.*
	Kr–3 × 4	do	26	0	*RR* × *RR.*
	Kr–4 × 3	do	9	0	*RR* × *RR.*
Cross with homozygous susceptible cabbage.	Kr–3 × C–131	do	26	0	*RR* × *rr.*

Plants from the hybrid progeny Kr–3×C–131 were saved and brought to flower in the greenhouse. The behavior of the progenies from self-pollination of these plants (KC–1, KC–2, etc.), as tested in the field and in the greenhouse, is shown in Table 7. As in Brussels sprouts, the progenies from self-pollination of the hybrids segregated in a ratio approximating 3 resistant to 1 susceptible. The trials in the field gave somewhat less than the expected number in the diseased class, whereas in the greenhouse trials the reverse was the case.

TABLE 7.—*Occurrence of yellows in F_2 progenies from a cross between a homozygous resistant kohlrabi plant (Kr–3) and a homozygous susceptible cabbage plant (C–131)*

Progeny No.	Tested in—	Number of plants		Deviation	Probable error	Dev. / P. E.
		Healthy	Diseased			
KC–1s	Field	31	7	2.50	±1.80	1.39
KC–2s	do	23	6	1.25	±1.57	.80
KC–4s	do	61	11	7.00	±2.48	2.82
	do.[a]	45	27	9.00	±2.48	3.63
	Greenhouse	98	42	7.00	±3.46	2.02
KC–5s	Field	5	2	.25	±.77	.32
KC–6s	do	20	9	1.75	±1.57	1.11
KC–7s	do	10	3	.25	±1.05	.24
KC–8s	do	62	13	5.75	±2.53	2.27
	do.[a]	41	21	5.50	±2.30	2.39
	Greenhouse	149	53	2.50	±4.15	.60
KC–9s	Field	22	2	4.00	±1.43	2.80
	Greenhouse	11	5	1.00	±1.17	.85
KC–10s	Field	37	11	1.00	±2.02	.50
	Greenhouse	43	15	.50	±2.22	.23
KC–11s	Field	68	7	11.75	±2.53	4.64
	Greenhouse	84	20	6.00	±2.98	2.01
KC–12s	Field	20	5	1.25	±1.46	.86
	Greenhouse	28	12	2.00	±1.85	1.08
KC–13s	Field	42	8	4.50	±2.07	2.17
	Greenhouse	31	15	3.50	±1.98	1.77
KC–14s	Field	55	14	3.25	±2.43	1.34
	do.[a]	48	19	2.25	±2.39	.94
	Greenhouse	139	59	9.50	±4.11	2.31
KC–15s	Field	14	3	1.25	±1.20	1.04
KC–16s	do	37	5	5.50	±1.89	2.91
KC–17s	do	47	6	7.25	±2.13	3.40
	Greenhouse	40	15	1.25	±2.17	.58
KC–18s	Field	24	4	3.00	±1.55	1.94
	Greenhouse	19	13	5.00	±1.65	3.03
Total in field		712	183	40.75	±8.74	4.66
Total in greenhouse		642	249	26.25	±8.72	3.01
Grand total		1,354	432	14.50	±12.34	1.18
Calculated (3:1)		1,340	446			

[a] Test made in 1931; other tests were made in 1930.

Back crosses of the hybrid plants (Kr–3×C–131) were made with homozygous susceptible cabbage (SP–5 and SP–9). The reaction of the progenies of this type are given in Table 8. The diseased class in the field trial of 1930 contained fewer plants than was expected on the basis of a 1 to 1 ratio, but the discrepancy is explained, as in Brussels sprouts, by the loss of members of the susceptible class in the yellows-infested seed bed. Further trials of three of these progenies were made in the field in 1931. Two segregated in an approximately 1 to 1 ratio; in the third, the number of diseased plants was higher than expected. In greenhouse trials all progenies tested showed approximately the same number in each class.

TABLE 8.—*Occurrence of yellows in progenies resulting from back crosses between F_1 hybrid plants (Rr) (from cross Kr–3 (RR)×C–131 (rr)) and plants of a homozygous susceptible cabbage line (SP)*

Progeny No.	Tested in—	Number of plants		Deviation	Probable error	Dev./P. E.
		Healthy	Diseased			
KC-1×SP-5	Field	35	15	10.00	±2.38	4.20
	Greenhouse	79	87	4.00	±4.35	.92
KC-2×SP-5	Field	30	16	7.00	±2.29	3.06
	do.[a]	57	53	2.00	±3.54	.56
	Greenhouse	173	133	20.00	±5.90	3.39
KC-3×SP-5	Field	31	18	6.50	±2.36	2.75
KC-4×SP-5	do	29	23	3.00	±2.43	1.23
	do.[a]	55	82	13.50	±3.95	3.42
	Greenhouse	74	64	5.00	±3.96	1.26
KC-5×SP-5	Field	42	26	8.00	±2.78	2.88
	do.[a]	33	35	1.00	±2.78	.36
	Greenhouse	33	26	3.50	±2.59	1.35
KC-6×SP-5	Field	35	17	9.00	±2.43	3.70
	Greenhouse	33	29	2.00	±2.66	.75
KC-7×SP-5	Field	21	15	3.00	±2.02	1.49
KC-8×SP-5	do	30	17	6.50	±2.31	2.81
	Greenhouse	30	28	1.00	±2.57	.39
KC-9×SP-5	Field	23	19	2.00	±2.19	.91
	Greenhouse	26	27	.50	±2.46	.20
KC-10×SP-5	Field	29	15	7.00	±2.24	3.12
	Greenhouse	30	29	.50	±2.59	.19
KC-11×SP-5	Field	32	21	5.50	±2.46	2.24
KC-12×SP-5	do	37	16	10.50	±2.46	4.27
	Greenhouse	74	89	7.50	±4.31	1.74
KC-13×SP-9	Field	30	24	3.00	±2.48	1.21
KC-14×SP-5	do	33	29	2.00	±2.66	.75
KC-15×SP-5	do	38	18	10.00	±2.52	3.97
KC-16×SP-9	do	25	25	0	±2.38	0
	Greenhouse	68	83	7.50	±4.14	1.81
KC-17×SP-9	Field	19	25	3.00	±2.24	1.34
Total in field		664	509	77.50	11.55	6.71
Total in greenhouse		620	595	12.50	11.76	1.06
Grand total		1,284	1,104	90.00	16.48	5.46
Calculated (1:1)		1,194	1,194			

[a] Test made in 1931; other tests were made in 1930.

DISCUSSION

The data seem to prove that resistance to the yellows organism is based on a single-factor difference in kohlrabi and Brussels sprouts, as has already been shown to be the case in both cultivated and wild cabbage.[8] Since all these plants belong to the composite species *Brassica oleracea*, it is reasonable to suppose that the same gene is responsible for resistance in all four subspecies. The results herein reported demonstrate the possibility of developing homozygous resistant lines of kohlrabi and Brussels sprouts by selection from individual survivors in commercial stocks grown upon soil thoroughly infested with the yellows organism.

SUMMARY

It has been shown that when commercial varieties of Brussels sprouts and kohlrabi were planted on yellows-infested soil certain individuals remained free from the disease throughout the growing season. When such individuals were self-pollinated the progenies of some proved to be completely resistant, whereas the progenies of others segregated in a ratio approximating 3 resistant to 1 susceptible.

[8] WALKER, J. C. Op. cit. (See footnote 2.)

When plants from completely resistant progenies were crossed with homozygous susceptible cabbage plants, resistance was found to be completely dominant in the F_1 generation. Progenies from self-pollination of F_1 hybrid plants when grown upon infested soil segregated into resistant and susceptible classes in the ratio of 3 resistant to 1 susceptible. When the F_1 hybrid plants were back crossed with susceptible cabbage plants, segregation of the progenies occurred in the ratio of 1 resistant to 1 susceptible.

These results indicate that, as already shown for both cultivated and wild cabbage, Fusarium resistance in Brussels sprouts and kohlrabi is based on a single-factor difference and is probably carried by the same gene in all four subspecies of *Brassica oleracea*.

The present report demonstrates the possibility of developing homozygous resistant lines of Brussels sprouts and kohlrabi by selection from resistant individuals grown on yellows-infested soil.

EFFECT OF FLUORINE ON THE NUTRITION OF SWINE, WITH SPECIAL REFERENCE TO BONE AND TOOTH COMPOSITION[1]

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INTRODUCTION

Numerous reports have appeared in the literature purporting to show the value of phosphoritic minerals as calcium and phosphorus supplements in animal nutrition. A great variance exists between the results obtained by different investigators. Forbes and others (*9*)[2] have inferred that the fluorine content of these naturally occurring products was the cause of the harmful and variable results obtained when these minerals were fed to livestock. Such an assumption seems to be fairly well grounded, since there is some correlation between the fluorine content of various grades of these minerals and the poor results obtained. However, the majority of the investigators have made no attempt to determine whether the feeding of fluorine salts would produce results comparable to those produced when the natural minerals were fed. In the present investigations a study was made of the comparative effects of flourine, in the forms of chemically pure sodium fluoride and the natural phosphate mineral, in the nutrition of swine, with special reference to the effect on bone and tooth composition.

REVIEW OF LITERATURE

Different investigators have shown that fluorine in one form or another may prove to be extremely toxic and very often fatal. Baldwin (*2*) and McNally (*24*) reported several cases of fluorine poisoning in man. Blaizot (*5*), Wieland and Kurtzahn (*39*) and Marcovitch (*25*) studied the lethal doses of different forms of fluorine for rabbits, while Heidenhain (*16*) reported on the lethal effects of sodium fluoride in dogs. Using sublethal doses of fluorine in different forms, Schulz and Lamb (*30*), Bergara (*3*), Sollmann, Schettler, and Wetzel (*32*), and McClure and Mitchell (*19*) observed an impairment of growth and feed consumption in rats.

The effects of fluorine on the various organs and tissues of the body have been studied by numerous investigators. Brandl and Tappeiner (*6*) could find no histological changes in the blood, liver, kidneys, or muscles of a dog fed varying amounts of sodium fluoride. The same investigators found no evidence of histological change in

[1] Received for publication Jan. 20, 1933; issued July 1933. The data in this paper are taken, in part, from a dissertation by C. H. Kick in partial fulfillment of the requirements for the degree of doctor of philosophy in the Graduate School of the University of Wisconsin.

[2] Reference is made by number (italic) to Literature Cited, p. 1035.

the bones, but reported the presence of crystals—presumably calcium fluoride—in the Haversian canals and in the porous bone near the epiphysis of the long bones. Sollmann, Schettler, and Wetzel (*33*) reported that they were unable to find histological lesions in rats fed 8 mg of sodium fluoride per kilogram of body weight daily for 9 weeks. Pitotti (*27*) observed a degeneration of the epithelium of the kidneys and a cloudy swelling of the liver in rabbits and guinea pigs fed lethal doses of sodium fluoride. Siegfried (*31*) noted that sodium fluoride and sodium fluosilicate caused a destruction of the epithelium of the intestines, even though these salts had been introduced into the body through other channels. Weinland (*38*) reported that the mucous membrane from the throat of a frog was killed by a 2.1 per cent solution of sodium fluoride. Grützner (*13*) noted that nerves were equally sensitive. Maumene (*26*) and Goldemberg (*11*) each reported that the feeding of sodium fluoride caused an increase in the size of the thyroid glands of dogs and rats, whereas Chaneles (*7*), and Tolle and Maynard (*36*) were unable to verify these findings.

The specific effect of fluorine on the teeth of rats has been shown by Schulz and Lamb (*30*), McCollum, Simmonds, Becker, and Bunting (*21*), Bergara (*3*), and Tolle and Maynard (*36*). The incisors became soft, elongated, and lost their normal pigmentation. Taylor (*35*), Huffman and Reed (*17*), and Bohstedt and his coworkers, as reported by Christensen (*8*) also reported that the teeth of dairy cattle became soft and showed excessive wear when rock phosphate containing fluorine was fed. The latter investigators also reported similar teeth changes in brood sows fed rations containing fairly liberal amounts of rock phosphate. The effect of fluorine ingestion on human teeth has been reported by Smith, Lantz, and Smith (*32*). These investigators found that children who drank water containing large amounts of fluorine developed soft teeth with mottled enamel. Similar observations were made by the California State Department of Health (*1*). The only known reference to any change in the chemical composition of the teeth due to fluorine ingestion is that of Sonntag (*34*), who reported an increase in the fluorine content.

Attempts to study the effect of fluorine feeding on bone formation have for the major part dealt with the use of rock phosphate as a mineral supplement in animal nutrition. Hart and his associates (*15*) reported improved bone formation when floats (rock phosphate) were used to supplement low phosphorus rations for pigs. Forbes and his coworkers (*9*), on the contrary, found that the feeding of rock phosphate to pigs produced less dense and weaker bones than when no minerals, or minerals practically free from fluorine, were fed. The weaker bones were characterized by maximum magnesium and phosphorus content and minimum calcium and carbon dioxide percentages. Reed and Huffman (*28*) demonstrated that the feeding of rock phosphate resulted in a thickening of the jaw and the metatarsal bones of dairy cattle. McClure and Mitchell (*19*) observed an increase in the ash percentage of bones, accompanied by a slight decrease in the calcium content of the ash, in rats on high fluorine rations. Tolle and Maynard (*36*), on the contrary, reported a decrease in the percentage of bone ash in rats fed a ration containing 1.8 per cent rock phosphate. The last-named investigators also reported that phosphatic limestone, containing approximately 1 per

cent fluorine, was equal to a mixture of limestone and steamed bone meal for growth and bone formation in the pig.

McClure and Mitchell (*20*) found that fluorine, in the form of rock phosphate or calcium fluoride, depressed calcium metabolism in the pig and that excessive fluorine intake also decreased growth and feed consumption.

That fluorine is a normal constituent of body tissues has been shown by Zdarek (*41*), Gautier (*10*), Wrampelmeyer (*40*), Jodlbauer (*18*), Harmes (*14*), Sonntag (*34*) and others. Sonntag (*34*) found that whereas normal teeth and bones of dogs contained not over 0.3 per cent fluorine, the bones of dogs fed sodium fluoride contained 1.73 per cent on the moisture-free and the fat-free basis, and the teeth 1.29 per cent on the dry basis.

EXPERIMENTAL PROCEDURE

Two separate experiments were carried out with growing pigs, housed indoors in concrete paved pens. Straw was used as bedding. At the termination of the experiment the animals were slaughtered and subjected to a routine post-mortem examination. The femurs and mandibles were removed for physical and chemical examinations. They were cleaned of adhering flesh and subjected to certain physical measurements, prior to the removal of the teeth for analytical purposes and the crushing and extraction of the femurs for chemical analysis. All the physical measurements and chemical determinations were made on the same femur from each animal in any particular experiment. The kidneys were fixed in 4 per cent formalin and subsequently examined histologically.

The maximum length and smallest diameter of the femurs were obtained by means of vernier micrometers. The volume of the femurs was determined by difference in the weights of the green, cleaned bone in air and when completely immersed in distilled water. Breaking strength determinations were made with an Olsen dynamometer. Calcium and magnesium were determined by McCrudden's (*22*, *23*) method, and phosphorus by the official gravimetric procedure. The carbon dioxide in the dry, fat-free bones was determined by the Van Slyke (*37*) method, and the volatilization method of Reynolds, Ross, and Jacobs (*29*) was used for the estimation on fluorine.

The same basal rations were used in the two experiments. Previous studies in this laboratory had shown that these rations were satisfactory for growing pigs when properly supplemented with calcium. The starting ration consisted of 55 parts yellow corn, 25 parts wheat middlings, 19 parts linseed meal, 0.5 part sodium chloride, and 0.5 part cod-liver oil. When the animals had attained a weight of approximately 125 pounds, the basal ration of all lots was changed at the same time to one consisting of 75 parts yellow corn, 14 parts wheat middlings, 10 parts linseed meal, 0.5 part sodium chloride, and 0.5 part cod-liver oil. The change in ration was made to widen the nutritive ratio, and conforms to good animal-husbandry procedure. The rations were hand-fed twice daily. The pigs were weighed individually every two weeks.

In the first experiment, which ran for 144 days; eight lots of eight pigs each, weighing at the start approximately 50 pounds each, were used. Four lots of pigs received the basal rations supplemented with 908 g of ground limestone, and 0, 30, 60, and 100 g of sodium fluoride

per 100 pounds of ration. Two more lots were fed the basal rations supplemented with 2 parts of different rock phosphates. Rock phosphate A was of Tennessee origin and analyzed 3.34 per cent fluorine, while rock phosphate B represented a pebble rock phosphate mined in Florida and contained 3.61 per cent fluorine. The pigs in another lot had their ration supplemented with equal parts of ground limestone and rock phosphate A, and the remaining lot received a ration that included 2 parts of steamed bone meal.

The mineral composition of these rations are presented in Table 1. The calcium: phosphorus ratios of the rations of the different lots were variable. However, other work in this laboratory indicates that the variations fall within the range of maximum performance and that the percentages of calcium and phosphorus, or the proportion in which they were present in the ration, were not limiting factors in the growth, or in the bone and tooth formation of these animals.

TABLE 1.—*Mineral composition of rations used for each of eight lots of pigs in Experiment 1*

[Upper figures represent starting ration; lower figures represent finishing ration]

Lot No.	Mineral additions to 100-pound basal ration	Calcium	Phosphorus	Magnesium	Fluorine	Ca:P ratio
		Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*
1	908 g ground limestone	0.802	0.527	0.269	(a)	1.5
		.766	.422	.212	(a)	1.8
2	908 g ground limestone; 30 g sodium fluoride	.802	.527	.269	0.029	1.5
		.766	.422	.212	.029	1.8
3	908 g ground limestone; 60 g sodium fluoride	.802	.527	.269	.058	1.5
		.766	.422	.212	.058	1.8
4	908 g ground limestone; 100 g sodium fluoride	.802	.527	.268	.097	1.5
		.766	.421	.211	.097	1.8
5	454 g ground limestone; 454 g rock phosphate, A	.786	.676	.254	.033	1.2
		.751	.570	.197	.033	1.3
6	908 g rock phosphate B	.772	.827	.236	.070	.9
		.736	.721	.180	.070	1.0
7	908 g rock phosphate A	.770	.824	.240	.065	.9
		.734	.719	.183	.065	1.0
8	908 g steamed bone meal	.735	.822	.240	(a)	.9
		.700	.717	.183	(a)	1.0

[a] Trace.

From the growth and feed-utilization data presented in Table 2, it is obvious that as the percentage of fluorine in the ration increased, the feed intake, the daily gains, and the feed utilization of the animals were materially reduced. These reductions occurred irrespective of whether the fluorine in the ration was derived from rock phosphate or sodium fluoride. The data, in general, substantiate the observations of other investigators that an excess of fluorine in the ration retards growth and feed consumption in various classes of animals.

TABLE 2.—*Gains and feed requirements of various lots of pigs in Experiment 1*

Lot No.	Fluorine in ration	Average initial weight	Average final weight	Average daily gain per pig	Average daily feed per pig	Feed required per 100 pounds of gain
	Per cent	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
1	(a)	54.6	204.6	1.04	4.92	472.4
2	0.029	52.0	192.0	.97	4.48	461.3
3	.058	54.0	182.6	.89	4.31	483.1
4	.097	52.5	138.0	.59	3.62	610.5
5	.033	54.0	196.0	.99	4.84	491.7
6 [b]	.070	51.1	139.4	.59	3.89	635.8
7	.065	53.1	130.3	.54	3.48	650.1
8	(a)	52.1	217.0	1.14	5.02	438.7

[a] Trace.

[b] 1 pig in lot 6 died at 103 days.

Daily observations of the different lots revealed that the pigs in the lots on high-fluorine rations, particularly lots 6 and 7 (2 parts rock phosphate) were consuming considerably more water than were those in the other lots. No attempts were made to record the comparative water consumption of the different lots in this experiment. It was also noted that several of the animals in the fluorine-fed lots manifested signs of stiffness and were rather reluctant to move. This was especially true in the higher fluorine lots. One pig in lot 6 (2 parts rock phosphate B) died at 103 days. Post-mortem examination showed a contracted, roughened, firm, pale kidney.

Gross examination of the femurs showed that those from lots 1 and 8 (2 parts limestone and 2 parts steamed bone meal, respectively) were smooth and dense in appearance, with a normal yellowish color and a definite luster, while those of the other lots were rough, lusterless, white in color, and with some exostoses. These conditions became more pronounced as the amount of fluorine in the ration increased. It is apparent from the data in Table 3 that the breaking strength of the bone is affected by high fluorine intake. Those rations that contained approximately 0.06 per cent of fluorine or more, either in the form of rock phosphate or sodium fluoride, significantly decreased the tensile strength of the femur. The data also indicate that excessive fluorine ingestion increases the diameter of the femur. This is particularly evident when the comparative length and weight of the bone are taken into account. The ash content of the femurs (Table 3) shows some variation. In general, the percentage of ash is lowest in the highest fluorine-fed lots. The difference in ash values are, however, only statistically significant in the case of lots 1 and 4 (control, and 100 g of sodium fluoride, respectively). Further experimental work is required before it can be stated with certainty whether or not excessive fluorine feeding will significantly lower the percentage of bone ash in pigs during short or long feeding periods.

TABLE 3.—*Physical measurements and ash analyses of the femurs of pigs in various lots in Experiment 1*

Lot No.	Fluorine in ration	Weight	Volume	Length	Smallest diameter	Breaking strength	Ratio of breaking strength to weight of bone	Ash	Grams of ash/cc volume
	Per cent	*Grams*	*Cubic centimeters*	*Centimeters*	*Centimeters*	*Pounds*		*Per cent*	
1	(a)	177	135	18.4	2.00	690±62	3.94	61.33±0.39	0.805
2	0.029	164	124	17.5	2.06	733±29	4.51	62.34±.27	.825
3	.058	167	131	16.8	2.21	647±34	3.92	60.50±.31	.770
4	.097	135	111	16.3	2.03	393±19	2.93	58.03±.29	.708
5	.033	160	126	17.1	2.12	766±31	4.81	61.86±.51	.760
6	.070	133	111	16.3	2.05	407±34	3.21	59.42±.68	.707
7	.065	134	109	16.1	2.01	456±40	3.34	60.78±.54	.743
8	(a)	177	134	18.3	1.95	841±55	4.80	61.61±.32	.816

[a] Trace.

The close correlation between the amount of ash per unit volume of bone and the breaking strength is of special interest. Apparently the ash-volume ratio is a more critical factor in determining the tensile strength of the femur than is the percentage of ash in the dry extracted bone.

The chemical analyses of the bone ash and dry extracted femurs, presented in Table 4, show that increasing percentages of fluorine in the ration had no significant effect on the percentage of calcium and phosphorus in the ash, whereas the percentage of magnesium tended to increase with increased fluorine intake, irrespective of the magnesium content of the ration. The carbonate content of the fat-free bones tended to decrease with increased fluorine intake, while the percentage of fluorine in the bone was directly proportional to the amount ingested.

TABLE 4.—*Chemical analyses*[a] *(per cent) of the femurs of pigs in various lots in Experiment 1*

Lot No.	Fluorine in ration	Calcium	Phosphorus	Magnesium	Carbon dioxide	Fluorine
1	(b)	38.39	17.48	0.790	2.76	0.039
2	0.029	38.50	17.99	.959	2.72	.534
3	.058	38.27	17.68	.972	2.37	.775
4	.097	38.43	17.62	1.141	2.34	1.108
5	.033	38.10	17.89	1.036	2.57	.594
6	.070	37.79	17.91	1.167	1.92	1.037
7	.065	37.92	18.14	1.137	2.06	1.093
8	(b)	38.31	17.75	.823	2.81	.036

[a] The calcium, phosphorus, and magnesium percentages are based on the bone ash; those of the carbon dioxide and fluorine are based on the dry, fat-free bone.
[b] Trace.

The mandibles of the fluorine-fed pigs showed the same thickened condition and rough, white, lusterless appearance that was noted in the femurs. Enlargement of the body of the bone and the appearance of exostoses became more evident with increased fluorine intake. No differences in the amount of wear of the teeth from the various lots were noted. However, there was a tendency for the teeth from the higher fluorine lots to chip more easily than those from the controls. Chemical analysis of the teeth did not show any significant difference in the percentage of ash or in the calcium, phosphorus, and magnesium content of the ash. (Table 5.) The carbon dioxide content of the teeth was not affected, except in lots 6 and 7 (2 parts rock phosphates A and B), which gave evidence of a slight decrease. The percentage of fluorine in the teeth was directly proportional to the amount present in the ration.

TABLE 5.—*Chemical composition*[a] *(per cent) of the teeth of pigs in various lots in Experiment 1*

Lot No.	Fluorine in ration	Ash	Calcium	Phosphorus	Magnesium	Carbon dioxide	Fluorine
1	(b)	74.04	35.83	17.48	1.45	2.03	0.083
2	0.029	74.96	36.32	17.77	1.54	2.09	.181
3	.058	74.17	36.83	17.86	1.63	2.07	.281
4	.097	74.69	36.99	17.88	1.53	2.15	.361
5	.033	74.84	36.67	17.66	1.51	2.11	.228
6	.070	74.44	36.70	17.57	1.50	1.83	.331
7	.065	75.17	37.02	17.35	1.56	1.95	.375
8	(b)	75.80	36.88	17.33	1.79	2.12	.092

[a] Calcium, phosphorus, and magnesium percentages are based on tooth ash; those of carbon dioxide and fluorine on dry, fat-free teeth.
[b] Trace.

Gross examination of the various organs at the time of slaughter revealed no abnormalities, with the exception of the kidneys from the pigs that had been fed rock phosphate. The kidneys were pale in color, contracted, and firm in texture, and their surfaces were

roughened by numerous small nodules and depressions. (Fig. 1, A.) The capsules were slightly thickened, and in some instances firmly adherent to the surface. Occasionally small cysts containing a clear or amber-colored fluid protruded above the surface of, or were more

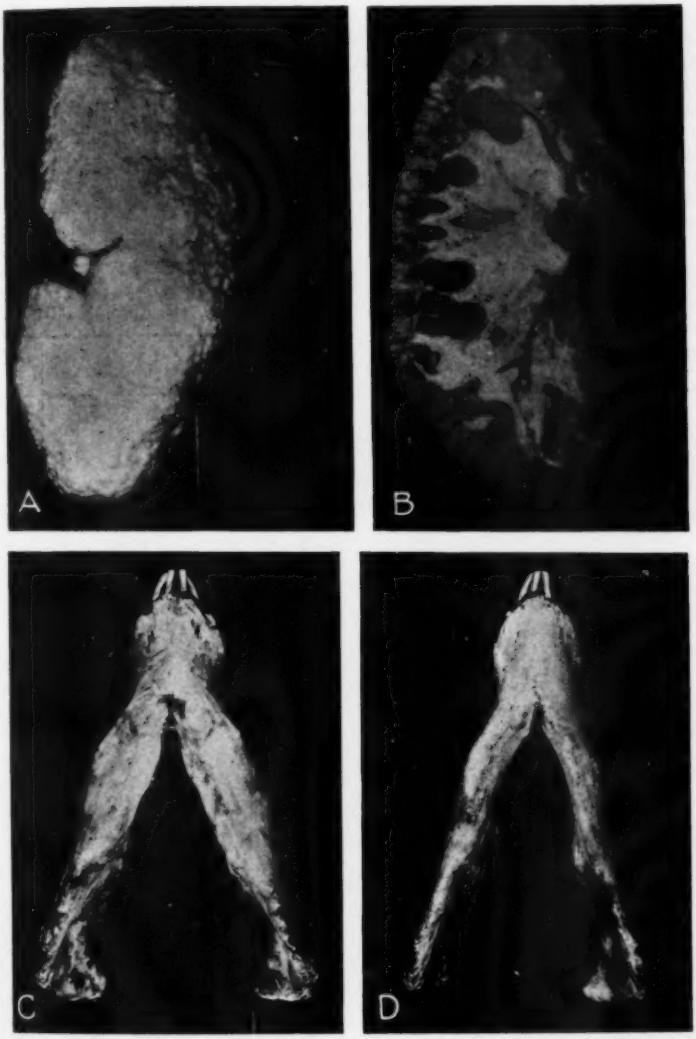


FIGURE 1.—A, External appearance of kidney from a pig that was fed 2 per cent rock phosphate; B, cross section of kidney from a pig that was fed 2 per cent rock phosphate; C, D, mandibles of pigs No. 76 of lot 4 and No. 58 of lot 1, showing increased thickness caused by the ingestion of fluorine

deeply situated in, the kidney. On section the cortex appeared reduced in width, and frequently the medulla contained considerable amount of fat. (Fig. 1, B.)

Microscopically the kidneys showed a nephritis with a varying degree of degeneration of the tubular epithelium and, as a terminal result, the replacement of many tubules and glomeruli with fibrous tissue. (Pl. 1.) None of the animals in the control or sodium fluoride-fed lots exhibited this condition.

In an attempt to confirm the results of the previous trial, and to study the effects of smaller amounts of fluorine in the ration, a second experiment, using six lots of eight pigs each, was started. The basal rations were the same as those used in the first test. The experiment ran for 160 days and was conducted under conditions similar to those in the first experiment. The mineral composition of the rations are presented in Table 6. The amounts of the phosphatic minerals and limestone were so adjusted that the percentages of calcium and phosphorus were the same in the rations of all lots. Fluorine was supplied in varying amounts in the form of sodium fluoride or rock phosphate.

TABLE 6.—*Mineral composition of rations used for each of six lots of pigs in Experiment 2*

[Upper figures represent starting ration; lower figures finishing ration]

Lot No.	Mineral additions to 100-pound basal ration	Calcium	Phosphorus	Magnesium	Fluorine	Ca:P ratio
		Per cent	*Per cent*	*Per cent*	*Per cent*	
1	454 g ground limestone; 454 g steamed bone meal	0.714	0.654	0.348	(a)	1.1
		.672	.556	.260	(a)	1.2
2	454 g ground limestone; 454 g steamed bone meal; 10 g sodium fluoride.	.714	.654	.348	0.010	1.1
		.672	.556	.260	.010	1.2
3	454 g ground limestone; 454 g steamed bone meal; 30 g sodium fluoride.	.714	.654	.348	.029	1.1
		.672	.556	.260	.029	1.2
4	454 g ground limestone; 454 g steamed bone meal; 60 g sodium fluoride.	.714	.654	.348	.058	1.1
		.672	.556	.260	.058	1.2
5	429 g ground limestone; 227 g steamed bone meal; 222 g rock phosphate.	.714	.654	.346	.016	1.1
		.671	.557	.258	.016	1.2
6	404 g ground limestone; 444 g rock phosphate	.714	.654	.343	.032	1.1
		.672	.557	.255	.032	1.2

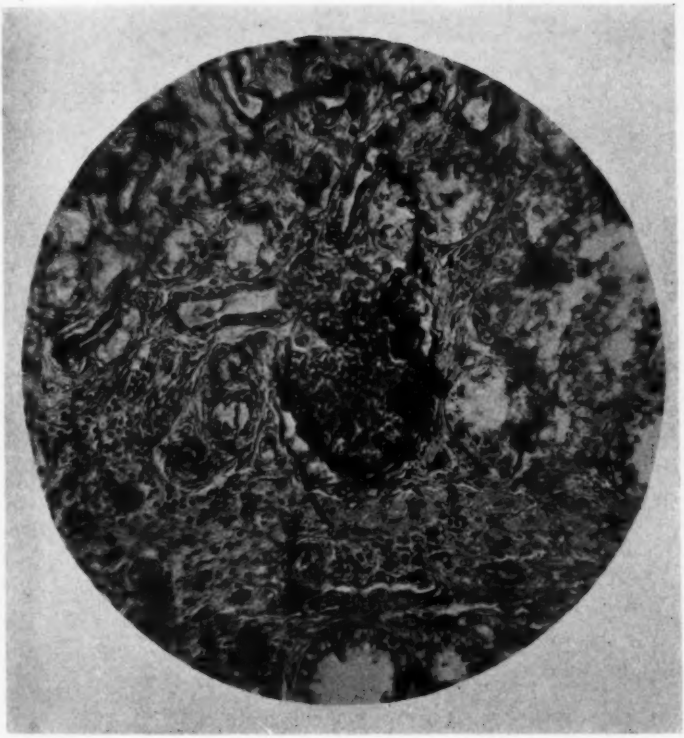
[a] Trace.

The gains and feed requirements of the different lots are recorded in Table 7. It is evident that when the fluorine content of the ration exceeded 0.029 per cent the rate of gain and the economy of gain were decreased. Smaller amounts of fluorine, either in the form of sodium fluoride or rock phosphate, appeared to be without effect on growth or feed utilization. These observations, in general, substantiate the results of the first trial and other unpublished data of this laboratory.

TABLE 7.—*Gains and feed requirements of various lots of pigs in Experiment 2*

Lot No.	Fluorine in ration	Average initial weight	Average final weight	Average daily gain per pig	Average daily ration per pig	Feed required per 100 pounds of gain
	Per cent	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
1	(a)	39.3	243.4	1.28	5.08	398.4
2	0.010	37.7	244.6	1.29	4.92	380.2
3	.029	38.8	213.6	1.09	4.26	389.9
4	.058	39.4	161.3	.76	3.41	450.2
5	.016	40.4	246.0	1.29	5.06	394.7
6	.032	40.4	219.4	1.12	4.85	434.0

[a] Trace.



Photomicrograph of a section of a kidney from a pig fed 2 per cent rock phosphate, showing characteristic degeneration and presence of fibrous tissue.

Again, in this experiment it was observed that the pigs on the high-fluorine rations consumed larger quantities of water. To check this observation the water and feed consumption of all lots were carefully recorded for two weeks. The results (Table 8) show that a high-fluorine intake caused increased water consumption per unit of live weight.

TABLE 8.—*Effect of fluorine intake on water consumption of pigs in various lots in Experiment 2*

Lot No.	Fluorine in ration	Feed consumed	Water consumed	Average weight	Water consumed per 100 pounds of live weight
	Per cent	*Pounds*	*Gallons*	*Pounds*	*Gallons*
1	(a)	945	165	212	77.83
2	0.010	964	156	208	75.00
3	.029	767	153	188	81.38
4	.058	471	159	144	110.41
5	.016	927	165	212	77.83
6	.032	817	168	190	88.42

[a] Trace.

As in the previous experiment, the femurs of the pigs that had received 0.029 per cent or more of fluorine in their ration were rough, white, and lusterless, whereas the bones from the pigs on lower fluorine rations appeared normal. The data presented in Table 9 again show an increase in the diameter and a reduction in the breaking strength of the femurs of the pigs on the high-fluorine rations. The percentage of ash was not significantly affected by fluorine feeding. However, as in the first experiment, the amount of ash per unit volume of bone was decreased with higher levels of fluorine intake.

TABLE 9.—*Physical measurements and ash analyses of the femurs of pigs in various lots in Experiment 2*

Lot No.	Fluorine in ration	Weight	Volume	Length	Smallest diameter	Breaking strength	Ratio of breaking strength to weight of bone	Ash	Grams of ash/cc volume
	Per cent	*Grams*	*Cubic centimeters*	*Centimeters*	*Centimeters*	*Pounds*		*Per cent*	
1	(a)	178	139	18.4	1.96	1,013±38	6.06	61.75±0.34	0.801
2	0.010	182	140	18.3	2.04	976±55	5.33	62.85± .42	.826
3	.029	168	132	17.3	2.12	871±42	5.25	62.46± .41	.792
4	.058	157	131	17.1	2.22	550±23	3.49	60.74± .51	.732
5	.016	176	138	18.1	2.03	1,050±58	6.17	62.04± .25	.796
6	.032	179	142	18.3	2.10	827±37	4.76	62.62± .30	.792

[a] Trace.

The data on the chemical analysis of the femurs (Table 10) show no significant differences in the calcium and phosphorus contents of the bone ash from the different lots, while the percentage of magnesium increased with increased fluorine intake. Again, the carbonate content of the dry, fat-free femurs was reduced by high-fluorine feeding, whereas the percentage of fluorine in the bone was directly proportional to the amount ingested.

TABLE 10.—*Chemical analyses* [a] *(per cent) of the femurs of pigs in various lots in Experiment 2*

Lot No.	Fluorine in ration	Calcium	Phosphorus	Magnesium	Carbon dioxide	Fluorine
1	(b)	37.61	18.52	0.919	2.93	0.057
2	0.010	37.60	18.25	.968	3.01	.316
3	.029	37.64	18.33	1.001	2.71	.671
4	.058	37.74	18.23	1.211	2.31	1.077
5	.016	37.72	18.18	1.043	2.88	.409
6	.032	38.18	18.95	1.102	2.78	.624

[a] Calcium, phosphorus, and magnesium percentages are based on bone ash; those of carbon dioxide and fluorine on the dry, fat-free bone.
[b] Trace.

Gross examination of the mandibles revealed the same rough, white, lusterless condition in the high-fluorine lots, as noted in the previous trial. No difference could be detected in the amount of wear of the teeth from the various lots, although it was observed that the teeth of the high-fluorine lots had a tendency to chip more easily than those from the control or low-fluorine lots. The rami of the mandibles were increased in diameter as a result of high-fluorine intake. (Fig. 1, C, D.) This enlargement of the mandibles also caused an increase in the width of the dental arch at the point of the second molar. It was also found that the buccolingual dimensions, taken at the positions of the three molars, increased in direct proportion to the amount of fluorine in the ration. The vertical dimensions, taken at the same points, showed no significant differences

The analysis of the teeth (Table 11) showed no significant difference in the percentage of ash or carbon dioxide on the dry, fat-free basis. Neither did the tooth ash show any variation in the amount of calcium, phosphorus, or magnesium. The only variable noted was in the fluorine content of the dry, fat-free teeth. The amount present was directly correlated with the percentage in the ration.

TABLE 11.—*Chemical composition* [a] *(per cent) of the teeth of pigs in various lots in Experiment 2*

Lot No.	Fluorine in ration	Ash	Calcium	Phosphorus	Magnesium	Carbon dioxide	Fluorine
1	(b)	73.49	36.74	17.86	1.65	1.76	0.043
2	0.010	74.39	36.99	17.84	1.67	1.66	.127
3	.029	73.96	37.05	17.65	1.60	1.76	.262
4	.058	73.93	36.69	17.71	1.66	1.76	.373
5	.016	74.60	36.77	17.70	1.70	1.64	.124
6	.032	74.21	36.82	17.06	1.74	1.65	.228

[a] Calcium, phosphorus, and magnesium percentages are based on tooth ash; those of carbon dioxide and fluorine on dry, fat-free teeth.
[b] Trace.

A post-mortem examination revealed no abnormalities in the various organs, with the exception of the kidneys of the pigs from lot 6 (approximately 1 per cent rock phosphate). These organs showed the nephritis noted in the animals in the previous trial. None of the kidneys of the pigs from the other lots showed any pathological change.

In a third experiment pigs were fed rock phosphate at levels of 1 and 2 per cent of their ration and sodium fluoride at levels of 30 and

60 g per 100 pounds of ration for two years or more, extending through the complete reproduction cycle. Upon post-mortem these pigs showed bone and kidney changes similar to, but more extensive than, those observed in the experiments reported herein. The condition of, and changes in, the teeth of these long-time fluorine-fed pigs were much more marked than those of pigs in the short-time experiments. The detailed findings of the tooth changes have been reported elsewhere (*4*). Suffice it to state that frequently the teeth of the high-fluorine-fed pigs were worn to the gums, and the pulp cavities were exposed. This condition of the teeth was reflected in the manner in which the pigs consumed their feed. Upon taking a mouthful of feed the pigs would throw their heads backward in what appeared to be an attempt to swallow the feed without allowing it to come in contact with the molar teeth. No noticeable effort was made to chew the feed. The same animals were reluctant to drink cold water. It was also found that sows reared and maintained on high-fluorine rations did not consume sufficient feed for good lactation or to prevent them from becoming unthrifty.

DISCUSSION

From the results of these experiments, it is evident that excessive fluorine in the ration exerts definite physiological effects upon swine. These effects, in general, were the same whether the fluorine was derived from rock phosphate or sodium fluoride. The only difference noted was the effect that liberal amounts of rock phosphate (1 per cent or more of the ration) exerted on the kidneys. Equivalent or even higher levels of fluorine, in the form of sodium fluoride, had no such effect. Two explanations present themselves as to the cause of this discrepancy. Either the naturally occurring product must contain some substance or material, other than fluorine, which causes a pathological change in the kidney, or the fluorine in rock phosphate is present in a more toxic form than in sodium fluoride.

The increased water consumption of the pigs on the high-fluorine levels may in part be accounted for by the results of Gottlieb and Grant (*12*). These investigators recently reported that the intravenous injection of sodium fluoride into dogs caused a marked diuresis. Although no urinary volume determinations were attempted in the present experiments, it was noted that the litter in the pens of the high-fluorine-fed pigs was much more soiled with urine than that in the other pens. A marked increase in urine volume must therefore be accompanied by an increased water intake in order to avoid a serious dehydration of the body tissues.

The outstanding effect of fluorine on the femurs of pigs, noted in these investigations, was the decrease in breaking strength of these bones. Although the bones of the animals which received the larger amounts of fluorine were larger in diameter and contained approximately the same percentage of ash, their tensile strength was significantly less than bones from those in the low-fluorine lots. Obviously, the breaking strength of a bone is influenced by factors other than ash content. The close correlation between the amount of ash per unit volume of bone and its breaking strength suggest that the ash to volume ratio is a better criterion of the tensile strength of a bone than is the percentage of ash. The fact that the weakest bones possessed the greatest diameter and contained the least ash per unit

of volume, suggests that fluorine may cause some change in the cellular structure of the bones.

The results of the effects of fluorine ingestion on the inorganic composition of the femurs substantiate the findings of Forbes and his associates (*9*), that the weak bones caused by rock-phosphate feeding are characterized by maximum magnesium and minimum carbon dioxide percentages, but are in disagreement with the report of the same investigators that the proportions of calcium and phosphorus are also changed. It is of interest that the high magnesium and low carbonate percentages were independent of the magnesium or carbonate contents of the rations, the source of calcium and phosphorus in the rations, and the form in which fluorine was ingested. This shows that excessive fluorine intake alters the inorganic composition of the bone. Whether this change in composition as a result of excessive fluorine ingestion is due, in part, to a partial replacement of the carbonate by the fluoride, or an actual shift in the percentages of the different bone salts normally present to compensate for the increased fluorine content, requires further detailed study.

The mandibles of pigs which had been fed toxic amounts of fluorine showed changes similar to those described by Huffman and Reed (*17*) in the case of dairy cattle fed rock phosphate. On cross section, it was observed that the marrow cavities were greatly enlarged without noticeable increase in the thickness of the bone wall. A marked difference was also noted between the types of bone marrow in the high-fluorine and the low-fluorine lots. The marrow of the low-fluorine lots was red, while that from the high-fluorine lots was pale yellow and appeared to have a decided increase in fatty material. The difference in the size of the marrow cavity and color and texture of the marrow was particularly evident in animals that were fed sodium fluoride or rock phosphate for an extended period.

It was evident that fluorine exerted a definite effect on tooth structure in swine. This fact was especially noticeable in animals fed fluorine for two or more years. These tooth changes were similar to those reported by Huffman and Reed (*17*) in the case of dairy cattle fed rock phosphate. The chemical analysis of the teeth did not reveal any striking differences in their inorganic composition, aside from the increase in the percentage of fluorine, the increase being directly correlated with the fluorine content of the ration, which substantiates the work of Sonntag (*34*) with dogs.

The results are in agreement with the work of other investigators with different species of animals, in that excessive fluorine in the ration decreases growth and feed consumption, and the efficiency with which the feed is utilized. The data, in general, show that when more than approximately 0.03 per cent fluorine is included in the ration the normal performance of the pig is retarded. This is especially true in case of long-continued fluorine feeding. Under these conditions, the feed consumption is impaired to such an extent in sows suckling pigs that lactation is adversely affected, and frequently the animals become so unthrifty that it is impossible to bring them back to good condition on the same feed.

It should be pointed out that the average daily calcium and phosphorus intake of the pigs in the different lots in the same experiment were not always uniform, for the reason that the percentages of these elements in the rations between lots varied, or the daily feed intake

between lots was not the same. The authors are of the opinion that these variations in calcium and phosphorus intake do not detract from the significance of the results obtained, in that the minimum requirements for these elements were amply satisfied in all instances. Forbes and his associates (*9*) and McClure and Mitchell (*20*) obtained good results with pigs on a daily intake of 5 to 7 g of calcium. In the experiments herein reported, the daily calcium intake was from 2 to 3 times that fed by the above-mentioned investigators, and in all probability the requirements of the pigs for calcium and phosphorus were not limiting factors in the results secured.

SUMMARY

The feeding to pigs of rations containing approximately 0.03 per cent or more of fluorine derived from rock phosphate or sodium fluoride impaired growth and feed consumption and lessened the efficiency with which the rations were utilized. The femurs of the pigs were characterized by an increase in the diameter of the shaft, a loss of normal color and luster, the presence of exostoses, and a decreased breaking strength. These changes became more pronounced as the fluorine content of the ration increased.

The bones weakened by fluorine feeding contained normal percentages of ash, calcium, and phosphorus, increased amounts of magnesium and fluorine, and decreased percentages of carbon dioxide. The increased magnesium and fluorine contents and the decreased carbonate content were directly correlated with the percentage of fluorine in the ration. The feeding of fluorine caused an increase in the size of the rami of the mandibles. This enlargement was due to an increase in the size of the marrow cavity rather than to an increase in the thickness of the wall. The type of marrow in the cavity was also changed.

Excessive amounts of fluorine in the ration when fed over long periods softened the teeth of pigs. The percentages of ash, calcium, phosphorus, magnesium, and carbon dioxide in the teeth were not significantly affected by fluorine feeding; however, the fluorine content was directly proportional to the amount fed.

The fluorine from rock phosphate and sodium fluoride exerted the same physiological effects on swine, with the exception that rock phosphate caused certain pathological changes in the kidneys. A nephritis with resulting induration of the kidney occurred in varying degrees in all pigs fed approximately 1 per cent or more of rock phosphate in their ration.

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VITAMIN C CONTENT OF BALDWIN APPLES AND APPLE PRODUCTS[1]

By C. R. FELLERS, *Research Professor*, M. M. CLEVELAND, *Fellow*, and J. A. CLAGUE, *Research Assistant, Department of Horticultural Manufactures, Massachusetts Agricultural Experiment Station*

INTRODUCTION

In spite of the importance of apple as a food, only a few investigations of its vitamin C content have been reported. A study of the literature failed to reveal any data bearing on the important Baldwin variety. Nor have apple cider and other apple products been carefully evaluted for vitamin content. Although Bracewell, Hoyle, and Zilva (*1*)[2] found that the Bramley Seedling variety grown in England protected 300-g guinea pigs when fed at a daily level of 3 g, Van Leersum and Hoogenboom (*9*), Givens, McClugage, and Van Horne (*6, 7*), Kohman, Eddy, and Carlsson (*8*), Hessler and Williams (reported by Campbell (*4, p. 68*)), and Hessler and Craig (reported by Campbell, (*3, p. 67–68*)) found that the protective amounts of various varieties of apples varied from 10 to over 40 g. At the present time the apple is not generally considered a particularly good source of vitamin C.

This paper presents the first results of a study now being made of the important apple varieties of the Northeast and the effect of various factors upon the vitamin content of apples and of products manufactured from apples.

VITAMIN C IN SPRAYED AND UNSPRAYED APPLES

In 1932, Nelson and Mottern (*10*) reported that lead arsenate sprays applied to orange trees considerably reduced the vitamin C content of the fruit. Since apples are almost universally sprayed with arsenic compounds and other toxic substances for insect and fungus control, comparisons were made in the present investigation between sprayed and unsprayed Baldwin apples. The apples for the experiment were obtained from orchards at Haydenville, Mass., and from the college orchard at Amherst, Mass. The usual spray schedule was followed, lime-sulphur and lead arsenate being used. The college orchard received eight and the Haydenville orchard seven sprays. The season was dry, hence there was a considerable spray deposit on the sprayed fruit when it was picked. From 0.005 to 0.008 grain of As_2O_3 per pound of fresh fruit was found on the sprayed fruit, but the unsprayed showed merely a trace of arsenic. The sprayed fruit was a deeper red and of better quality than the unsprayed. However, only sound fruits were used in the feeding experiments. The apples were stored at 36° F. until the test was concluded. Examination was begun in October, 1931, immediately after harvest.

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[2] Reference is made by number (italic) to Literature Cited, p. 1045.

The quantitative animal feeding method of Sherman, La Mer, and Campbell (*11*) was followed, except that the guinea pigs were fed in proportion to their weight; that is, if an animal weighing 300 g received 3 g of apple daily, one weighing 400 g would receive 4 g of apple. This method is believed to be fairer than feeding the same weight of food regardless of the animal's weight. At least three animals housed in individual wire cages, were used for every test. Radial sectors of apples were fed because of the variation in vitamin C content in different parts of the apple (*2*, *5*).

The basal ration consisted of 58 per cent equal parts of rolled oats and wheat bran, 30 per cent of vitamin-C-free baked milk powder, 10 per cent butterfat, 1 per cent each of cod-liver oil and salt. This basal ration and water were kept before the animals at all times. However, the guinea pigs were forced to derive all their vitamin C from apples or apple products.

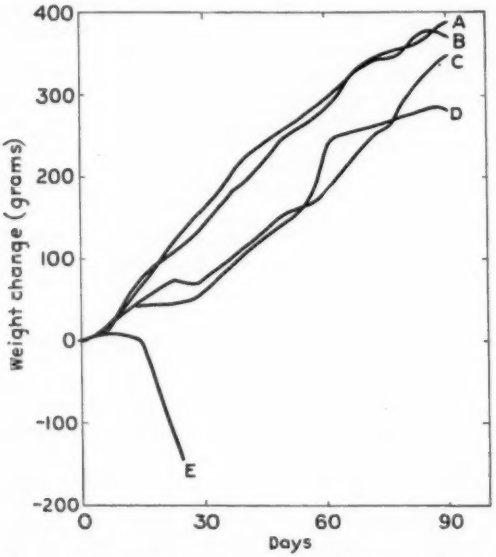

FIGURE 1.—Results of feeding guinea pigs sprayed and unsprayed Baldwin apples from Haydenville and Amherst, Mass., as the sole source of vitamin C: A, 4 g sprayed apple (Haydenville) fed daily, scurvy score, 0; B, 5 g sprayed apple (Amherst) fed daily, scurvy score, 0; C, 5 g unsprayed apple (Amherst) fed daily, scurvy score, 0; D, 4 g unsprayed apple (Haydenville) fed daily, scurvy score, 0; E, negative control, scurvy score, 10

At the end of the feeding period all animals were chloroformed and carefully examined for lesions of scurvy. Negative controls died in from 26 to 33 days with an average Sherman scurvy score of 16. A normal animal has a score of 0, while the maximum for extremely severe scurvy is 24.

The significant data are presented graphically in Figure 1. Apples from trees carefully sprayed all season are fully as rich in vitamin C as apples from unsprayed trees. In fact, the animals receiving sprayed fruit showed slightly larger weight gains than those receiving the unsprayed. Four grams daily of either sprayed or unsprayed Baldwin apples per 300-g guinea pig gave excellent weight gains and full protection from scurvy.

Two additional series of animals were fed 7 g of sprayed and unsprayed Baldwin apples from Amherst. The average weight gains per animal after 90 days were 381 and 430 g respectively, and there was no evidence of scurvy at autopsy. The data thus show no decrease of vitamin C in the sprayed fruit. In fact in two of the three tests the sprayed fruit appeared to contain slightly more vitamin C than the unsprayed.

VITAMIN C IN APPLES STORED FOR DIFFERENT LENGTHS OF TIME

Sprayed Baldwin apples grown on the college farm and stored at 36° F. were used to determine the effect of storage on vitamin C. The examinations for vitamin C were made in October immediately following harvest, after 3 to 5 months in storage, and finally after 8 to 10 months. Figure 2 shows the results obtained.

Four grams of fresh apple possessed approximately the same antiscorbutic potency as 5 g of 4-months-old apple or 6 g of 9-months-old fruit. Similarly, 3 g of apple in storage 4 months gave better growth and protection than 4 g after 9 months. After 9 months the loss in vitamin C was about 33 per cent. Baldwin apples apparently retain a substantial part of their vitamin C for several months; that is, during the season in which they are eaten in largest quantities. Bracewell, Kidd, West, and Zilva (*2*), and also Van Leersum and Hoogenboom (*9*) found no loss in vitamin C of apples during storage, but Hessler and Craig, as reported by Campbell (*3*), found a loss of fully 30 per cent in Jonathan apples held in storage about 5 months.

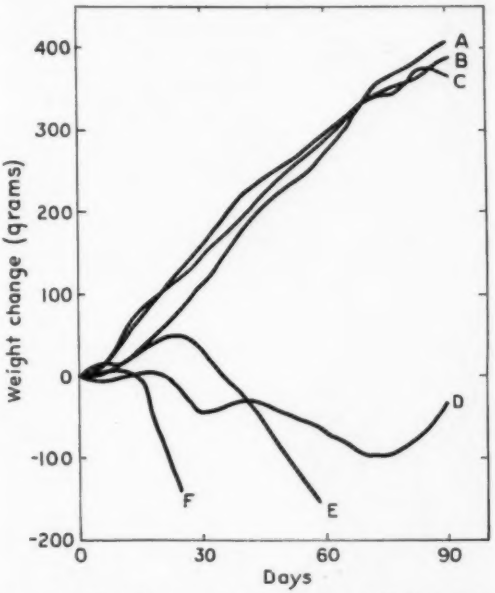

FIGURE 2.—Effect of storage on the vitamin C content of Baldwin apples as shown by the results of feeding them to guinea pigs as the sole source of vitamin C: A, 6 g apple stored 9 months fed daily, scurvy score, 0; B, 4 g fresh apple fed daily, scurvy score, 0; C, 5 g apple stored 4 months fed daily, scurvy score, 0; D, 3 g apple stored 4 months fed daily, scurvy score, 5; E 4 g apple, stored 9 months fed daily, scurvy score 13; F, negative control, scurvy score, 10

VITAMIN C IN APPLE JUICE AND PRESERVED CIDER

Apple juice was extracted daily from sprayed Baldwin apples which had been in storage 9 months and whose protective dose was approximately 6 g. The small centrifugal extractor shown in Figure 3 was used to extract the juice. The yield of juice averaged 70 to 80 per cent of the weight of the apple. The juice was pale green in color when first extracted but oxidized to a deep yellowish brown after 24 hours.

By the use of a hydraulic press cider was prepared from the apples that had been in storage at 36° F. for 4 months. Guinea pigs fed 5 g daily of these apples were fully protected from scurvy. The cider was divided into two portions. One was heated to 170° F. and allowed

to settle at 36° for 12 hours, siphoned into pint bottles, sealed with crown caps, and pasteurized for 20 minutes at 160°; the other was benzoated by adding sodium benzoate sufficient to give a concentration in the cider of 0.1 per cent. Both lots were stored in 1-pint bottles at 36°. It was necessary to make up a second batch of benzoated cider after the experiment had been in progress 40 days. The effect of feeding this freshly prepared cider is evident by the marked rise in Figure 5, C, at the 40 to 45 day interval. All juices and cider were fed by pipette, so that each animal received a known amount each day. (Fig. 4.)

FIGURE 3.—Small centrifugal extractor used in preparing the apple juice

The significant data are presented in Figure 5.

The animals receiving 9 g (not shown in fig. 5) and 6 g daily of freshly extracted apple juice were well protected against scurvy and showed large gains in weight. Three grams of the fresh juice, however, did not afford protection. Since 6 g of the whole apples afforded protection, it appears that freshly extracted juice is practically as rich in vitamin C as the apple itself. Nine grams of 1-day-old juice also afforded full protection, showing that the juice retains a substantial part of its vitamin C for at least 24 hours. Lesser amounts were not evaluated.

Pressed cider differs from extracted cider in both appearance and flavor. There is greater opportunity for oxidation to take place in the pressed product. The benzoated cider possesses moderate antiscorbutic properties for several days after manufacture but gradually loses this property on storage. Eight grams fed daily failed to support growth or give protection from scurvy. Probably 10 to 15 g would have been required. As pointed out previously, the temporary upward trend after 40 days in Figure 5 indicates increased growth as a result of feeding freshly prepared cider. No animal fed 4 g daily survived for more than 60 days.

Pasteurized cider when fed at the 8-g level showed practically no protective value and was little better than the negative controls. There is a marked loss in vitamin C when Baldwin apples are manufactured into benzoated or pasteurized cider. Unless the juice is freshly extracted from apples, it is likely to contain but little vitamin C.

VITAMIN C IN CANNED APPLE SAUCE

The vitamin C content of two kinds of Baldwin apple sauce was determined. Unstrained, "lumpy" or rough sauce, was prepared from peeled and cored fruit. The waste was 23 per cent. Sugar equivalent to 18.7 per cent of the weight of prepared apples and water equivalent to 13 per cent was added and the sauce was cooked in a loosely covered kettle for 6 minutes. Since the yield was exactly the weight of the prepared apples, 10 g of the finished sauce was practically equivalent to 8 g of apple. The sauce was packed into half-pint jars, pasteurized at 170° F. for 20 minutes, and immediately cooled.

FIGURE 4.—Pipette method of feeding apple juice and cider to guinea pigs

The smooth or strained apple sauce was prepared by cooking quartered unpeeled Baldwin apples until soft. Twelve per cent by weight of water was added before cooking. The mass was pulped while hot in a tomato pulper, 19 per cent sugar was added, and the sauce was packed hot into half-pint glass jars and pasteurized at 170° F. for 25 minutes. The sauce was stored at 36° until used, a new jar being opened every other day. Most of the guinea pigs ate the sauce greedily; those that did not were eliminated from the experiment. The graphs representing the collected data are shown in Figure 6.

In general, canned apple sauce does not retain much of the vitamin C of the fresh apple. Strained sauce, even when fed at 10-g levels

was little better than the negative control. Certainly the quantity of strained apple sauce necessary to protect against scurvy would be very high. The unstrained sauce was somewhat richer in vitamin C, but as much as 10 g was not nearly enough to protect the animals against scurvy or to maintain their weight. Neither style of sauce, as prepared in this experiment, can be considered of appreciable antiscorbutic value. These results are in accord with those of Hessler and Williams (*4*), who found that Johnathan apple sauce contained practically no vitamin C, and with those of Kohman, Eddy, and Carlsson (*8*) who obtained similar results with Yellow Newtown (Albemarle Pippin) and Stayman Winesap.

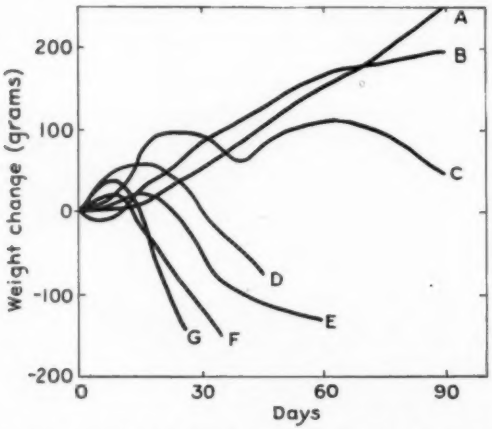

FIGURE 5.—Results of feeding guinea pigs Baldwin apple juice and apple cider as the sole source of vitimin C: A, 9 g 1-day-old apple juice fed daily, scurvy score, 0; B, 6 g fresh apple juice fed daily, scurvy score, 1.5; C, 8 g of benzoated cider fed daily, scurvy score, 10; D, 3 g fresh apple juice fed daily, scurvy score, 10; E, 4 g benzoated cider fed daily, scurvy score, 14; F, 8 g pasteurized cider fed daily, scurvy score, 14; G, negative control, scurvy score, 10

SUMMARY

The Baldwin apple grown in Massachusetts is a good source of vitamin C, about 4 g per 300 g of body weight sufficing to maintain growth in guinea pigs and to protect them fully from scurvy.

In two tests, apples from completely sprayed trees contained as much or possibly more vitamin C than apples from unsprayed trees.

In 4 to 6 months of storage at 36° F. Baldwin apples lost about 20 per cent of their vitamin C content; in 8 to 10 months the loss was nearly 40 per cent.

Freshly expressed Baldwin apple juice was found to be nearly as rich in vitamin C as the fresh apple. Little loss occurred during the

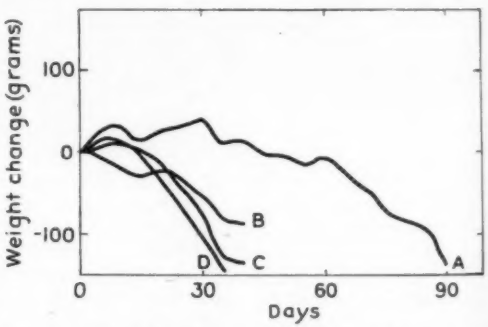

FIGURE 6.—Results of feeding guinea pigs Baldwin apple sauce as the sole source of vitamin C; A, 10 g unstrained apple sauce fed daily, scurvy score, 9; B, 5 g unstrained apple sauce fed daily, scurvy score, 13; C, 10 g strained apple sauce fed daily, scurvy score, 14; D, 5 g strained apple sauce fed daily, scurvy score, 14

first 24 hours after extraction. Benzoated or pasteurized ciders over 48 hours old, however, failed to retain an appreciable quantity of vitamin C.

Canned Baldwin apple sauce, either strained or unstrained, proved to be a poor source of vitamin C. The unstrained sauce was somewhat superior to the strained.

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SOMATIC SEGREGATION IN A SECTORIAL CHIMERA OF THE BARTLETT PEAR[1]

By V. R. GARDNER, *Director*, J. W. CRIST, *Research Assistant Horticulturist*, and R. E. GIBSON, *Michigan Agricultural Experiment Station*

INTRODUCTION

Mention is made in some of the older European pomologies of a considerable number of striped, banded or "panache" varieties or strains of pears. Apparently they never assumed much commercial importance and even academic interest in them must have largely disappeared, for more recent treatises have been inclined to overlook them and a search to-day would probably reveal the fact that most of them have disappeared from cultivation. Descriptions vary in their completeness, but it is evident that the fruits themselves were generally characterized by alternating sectors of the normal green and of yellow skin, extending from stem to calyx lobes, and that at least in many instances the bark of the shoots was similarly striped. Historical data pertaining to many of these sports are likewise incomplete, but the presumption is that most, if not all, originated as bud sports from normal solid green or self-colored varieties. Undoubtedly they would be now classified as sectorial chimeras.

In the summer of 1912 one of the authors of this article, in company with Dr. E. J. Kraus, then of the Oregon Agricultural Experiment Station, found a limb sport of this type in a tree of the Bartlett variety, near Medford, Oreg. Buds of this limb sport, set on quince stock on the grounds of the Oregon station at Corvallis, produced striped fruit like that borne by the original limb sport. No note was made at the time the original limb sport was found as to whether more or less than half of the surface of the fruits or of the shoots was yellow, or on the color distribution of either fruits or shoots as grown at the Oregon station. The sport was simply observed and propagated as a striped form. In 1923 scions obtained from the Oregon station trees were top grafted on some young Kieffer pear trees growing in the orchard of the Michigan experiment station, and the resulting grafts (four on one tree and two on another) have in turn furnished stock for more recent propagations. A study of the Michigan-grown stock of this strain has furnished the data relating to bud-sport origin reported in this paper.

DESCRIPTION OF MATERIAL

This striped bud sport of the Bartlett pear is apparently fairly representative of bud sports of similar type listed in the older pomologies. The developing fruits show alternating vertical stripes of yellow and green, the individual stripes being of various widths.

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(Fig. 1.) In some specimens the green predominates, in others the yellow. For the most part each stripe is continuous from base to apex of fruit, though many are broken, being green at the basal end and yellow at the apical end, or vice versa. This striping is clearly evident when the developing fruits are less than a quarter of an inch in diameter. As the fruits approach maturity, the stripes become less distinct because of the gradual disappearance of the green pigment. The fruit stems are not striped but are very much lighter in color than those of normal Bartletts, being distinctly yellowish in cast.

The young shoots of this sport similarly show an alternate striping with green and yellow; this condition likewise characterizes the new growth of the spurs. Toward the end of the growing season as the epidermis cracks and weathers and the corky layer of the cortex

FIGURE 1.—Typical specimens of the striped Bartlett, fully grown but still firm, and before the normal green color changes to yellow

becomes exposed, the striping disappears and the year-old shoots can not be readily told from those of a normal Bartlett. The leaves of the bud sport show no visible evidence of variegation and appear to be as large and as green as those of the normal unstriped form.

In a general way both fruits and shoots of the top grafts in the orchard of the Michigan station closely resemble those of the original limb on the parent tree near Medford, Oreg.

EXPERIMENTAL PROCEDURE

COLOR STRIPING OF SHOOTS

After the top grafts at the Michigan station had made two or three years' growth, it was noted that certain of the striped shoots on tree 1 were predominantly yellow, their green stripes being reduced to narrow

vertical lines and constituting not more than 10 per cent of the surface of the shoots; other shoots were predominantly green, their yellow stripes being similarly reduced to narrow bands, but constituting perhaps one-fourth of the total surface. Buds were selected from several of these shoots showing different proportions of the two color stripes and were set in seedlings pear stocks to determine whether it is possible to segregate from this striped strain other strains or substrains distinct in the relative amounts of green and yellow pigment in their bark.

Nursery trees grown from buds cut from striped shoots in which the green tissue predominated grew satisfactorily, though more slowly than adjoining trees of the normal Bartlett. Those grown from buds cut from striped shoots in which the yellow predominated made a very slow growth and at the end of the first season in the nursery were little over half the size of normal stock. (Fig. 2.) At the end of the second year in the nursery the differences were still more pronounced, the trees from the predominantly yellow buds stocks being very small, much-branched and having the general appearance of inferior seedlings, though they had received the best of care. Any nurseryman would classify them as culls, and it is doubtful if any experienced propagator or pomologist would recognize them as being of the Bartlett variety.

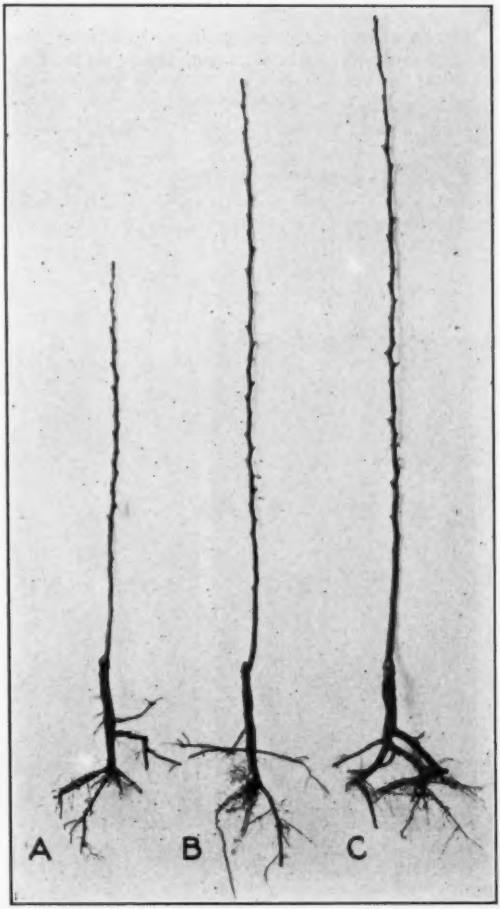

FIGURE 2.—Typical 1-year-old nursery trees of Bartlett selection: A, Striped form in which yellow color predominates; B, striped form in which green color predominates; C, normal trees with solid green bark. Note differences in size

The best of the 2-year-old nursery trees of these predominantly yellow selections were set out in the orchard in the spring of 1928,

along with some of those of the striped but predominantly green type, and some of the normal Bartlett for comparison. Several of those of the predominantly yellow type died; those that lived have made a comparatively weak growth. Figure 3 shows a representative tree of each selection after two years' growth in the orchard. After five years' growth in the orchard the difference in size between these groups of trees, though still great, was less pronounced than at the end of the first two years.

The marked differences in vegetative growth between these two striped strains and between them and the normal Bartlett, even

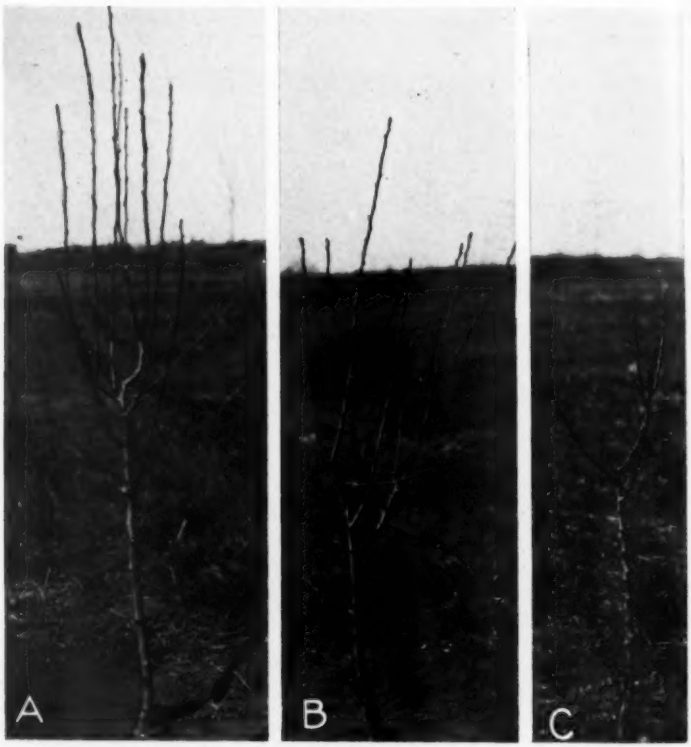

FIGURE 3.—Typical 2-year-old orchard tree of Bartlett selection: A, A normal all-green tree; B, a striped form with the green predominating; C, a striped form with the yellow predominating

though there were no apparent differences in size, thickness, or color of leaves, suggested the desirability of chlorophyll determinations on both leaves and bark of the shoots. Such determinations were made on young nursery stock of the three strains, samples being taken July 11 and August 13, 1932. The data are presented in Table 1. It is clear that, even though to all appearances the leaves of the two striped forms were as dark green as those of the check, or normal Bartlett, they actually contained distinctly less chlorophyll. The bark of the

striped strain in which the yellow color predominated was very low in the green chlorophyll pigments, and it likewise contained much less xanthophyll and carotin than did the bark of the normal Bartlett shoots. The bark of the striped shoots in which the green color predominated showed an intermediate condition. Incidentally these analyses, together with the growth records of the nursery and young orchard trees, suggest that the bark is a more important contributing factor in general vegetative growth and development than has been commonly thought.

TABLE 1.—*Chlorophyll and yellow pigment content of leaves and bark of shoots of normal and striped Bartlett strains*

[Expressed in terms of milligrams per 10 g of fresh material]

Date and strain	Chlorophyll (A+B)		Xanthophyll		Carotin		Total yellow pigments	
	Leaves	Bark	Leaves	Bark	Leaves	Bark	Leaves	Bark
July 11, 1932:								
Normal solid green Bartlett	15.02	4.44	1.27	0.21	1.18	0.24	2.45	0.45
Striped, with green predominating	9.66	3.27	1.18	.15	.77	.26	1.95	.41
Striped, with yellow predominating	9.63		1.16	.02	.95	.03	2.11	.05
Aug. 13, 1932:								
Normal solid green Bartlett	25.51	3.68	1.92	.20	.90	.15	2.82	.35
Striped, with green predominating	21.39	2.94	1.49	.11	.91	.09	2.40	.20
Striped, with yellow precominating	18.54	2.65	1.77	.09	.96	.06	2.73	.15

TABLE 2.—*Production of shoots and fruits of different color types by striped Bartlett grafts in 1932*

Color type of shoots and fruits	Number of shoots and fruits by tree and branch indicated					
	Tree 1, branch A	Tree 1, branch B	Tree 1, branch C	Tree 1, branch D	Tree 2, branch A	Trees 2, branch B
Shoots:						
Predominantly yellow	13	25	35	19	29	0
Predominantly green	5	7	3	3	4	1
Solid green	3	0	1	[a] 6	7	0
Fruits:						
Predominantly yellow	52	30	10	150	34	27
Predominantly green	22	7	8	95	41	87
Solid green	3	0	0	[b] 32	0	3

[a] Including shoots produced by the lower branch that had reverted to the normal Bartlett type.
[b] Including fruits produced by the lower branch that had reverted to the normal Bartlett type.

The success that attended the segregation of the original striped Bartlett into two striped color strains led to a careful scrutiny of all the shoots on the two trees in the orchard at East Lansing in the summer of 1932 to determine whether or not further segregation was taking place. The results of the observations are presented in Table 2. Most of the shoots were striped, but on four of the original six grafts one or more all-green shoots were produced, that is, in these cases there had been a complete reversion to normal. Of the 144 striped shoots on these 6 top grafts, 121 were classified as having yellow predomi-

nating, 23 as having green predominating. There seems to be no definite proportion of pure green or of principally green segregates characterizing all the grafts. One summer shoot (fig. 4) had its growth stopped in early June and then produced three secondary lateral branches, one of which was pure green, the second striped with green predominating, and the third striped with yellow preodminating. Here is a case of both partial and complete color segregation in branches arising from successive nodes on the same shoot. An even more interesting case of color segregation, this one taking place in a single shoot, is illustrated in Figure 5. In this instance the entire

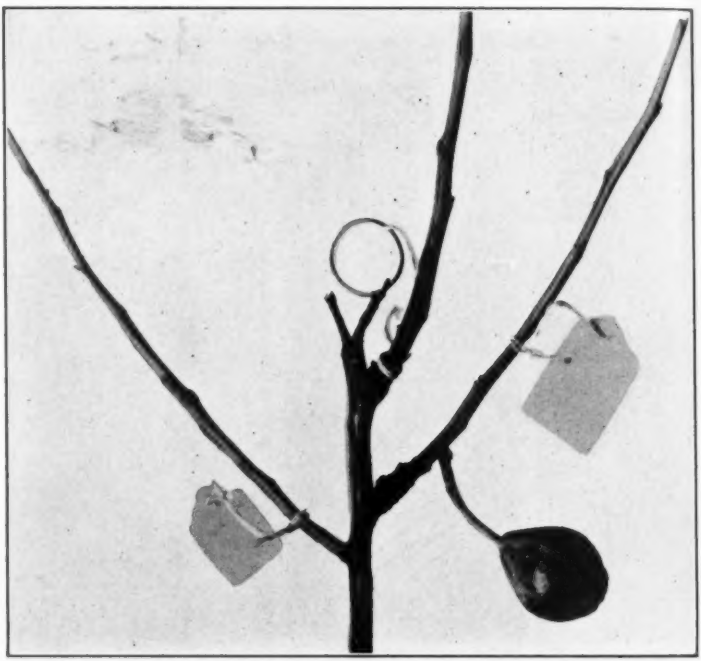

FIGURE 4.—A striped shoot of the striped Bartlett that had its growth stopped in midsummer and then gave rise to three lateral branches. The one at the left is striped but predominantly green; the one at the right is likewise striped but predominantly yellow; the one in the center is the normal solid green

shoot was striped; its basal third was predominantly yellow, the green stripes being reduced to mere pencillike lines; its median section was predominantly green, the yellow stripes being reduced to mere lines; the apical third was predominantly yellow, like the basal third. A close inspection of Figure 5 shows that these color changes occur at the nodes. A vertical green stripe that traverses a number of nodes and internodes may be replaced by a vertical yellow stripe that traverses the next one or more internodes, or vice versa; or a broad green and narrow yellow stripe that traverses one or more internodes may be replaced by a narrow green and broad yellow stripe at some node, or vice versa. One other shoot was found (besides that in fig. 5) in which there was a similar change from internode to internode in the

relative proportions of green and yellow, though none was found in which one or more internodes of an otherwise striped shoot were pure green or in which one or more internodes of an otherwise pure green shoot were striped. The 1932 records of shoots of these six top grafts would therefore seem to indicate that this particular striped strain is, at least from a vegetative standpoint, in a more or less inconstant or ever-sporting condition and raise a question as to whether it can ever be fixed or segregated into constant substrains. Fortunately some light is thrown on these questions by the progeny trees propagated from two of these six top grafts. Altogether, several hundred nursery trees have been grown from these selections, and a number have been planted in the orchard and carried along until they are now 5 years of age. All trees thus far grown from buds cut from shoots that were striped, but with the yellow stripes predominating, have produced shoots that almost without exception have been like the parent shoots. Those that have grown from buds cut from shoots that were striped, but with the green stripes predominating, have for the most part produced shoots that similarly were like the parent bud sticks, but there have been a few reversions to the pure green normal Bartlett form, and there has likewise been some segregation of striped and predominantly

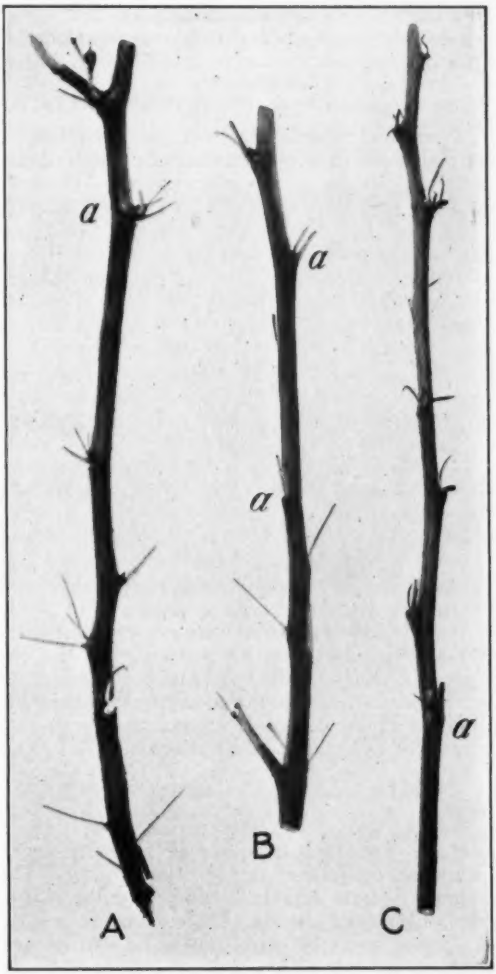

FIGURE 5.—Basal (A), median (B), and subterminal (C) sections of a single shoot of the striped Bartlett in which the basal section is predominantly yellow, the median section predominantly green, and the subterminal section predominantly yellow. Note the color changes taking place at certain of the nodes (*a*), a green stripe traversing one or several internodes being replaced by a yellow stripe, or vice versa

yellow types. The parent form, as found in Oregon, plainly was not constant or fixed. The subtypes (except for the reversion to the normal all-green Bartlett type) that have segregated from it are likewise not entirely fixed; but they are nevertheless much more constant, and experience with them indicates that they can be kept reasonably constant by suitable care in the selection of bud wood—and only in that way.

COLOR STRIPING OF FRUITS

Year after year it has been noted that the fruits themselves of the striped sport vary considerably in width of the alternating yellow and green sectors and in the percentages of the surface covered by the two colors. Not until 1932 were detailed records made relating to this color distribution. They are summarized in Table 2. Considering the crop as a whole, there were many more of the fruits in which the yellow predominated, just as in the shoots, though there was no uniformity in percentages between the different branches. The fruits borne by successive spurs on the same year's growth were in some cases all of one type, and in others presented all possible combinations. In some instances where two fruits were borne by one spur they were alike in color markings, in others one was predominantly green while the other was predominantly yellow. In one case one of a pair coming from a single flower cluster was striped and the other was solid green, a complete reversion to the normal parent Bartlett form. Apparently the successive nodes of the fruit-cluster base present the same opportunity for variation in the width of sectorial color stripes as is presented by successive nodes of the normal vegetative shoot. One whole branch (from graft 1D) that developed from the basal bud of the original scion showed complete reversion to the normal Bartlett type, producing solid green shoots and solid green fruits only, while the main growth of this graft, coming from the upper bud of the scion, has been producing the characteristically striped fruits. Evidently this one branch, in its origin and subsequent behavior, is comparable to one of those shown in Figure 4, and the parent scion for graft 1D corresponded closely to the upper 4 inches of the primary shoot shown in Figure 4.

SHAPE OF FRUIT

The Bartlett pear, like certain other pear varieties, presents considerable variation in shape of fruit, though, so far as the writers are aware, evidence has not been presented showing that the variety presents definite dimorphism or polymorphism in this respect. However, close examination of the fruits borne by the six top grafts of its striped sport in the experiment station orchard at East Lansing would suggest the existence of a dimorphic or possibly polymorphic condition. (Fig. 6.) It was therefore thought advisable in 1932 to keep separate the crops as harvested from the six grafts, measure each fruit, and calculate its form index. Table 3 shows the frequency distribution of these form indices (obtained by dividing the total axial by the total transverse diameter, each measured to the closest eighth of an inch). What the writers would consider an ideally shaped, typical, or normal Bartlett has a form index of approximately 1.25 to 1.35, that is, its axial diameter is about a quarter to a third

greater than its transverse diameter. A typical Kieffer pear has a form index of approximately 1.00. It will be noted that two of these striped Bartlett grafts (2A and 2B) produce fruits more or less closely approaching the typical Kieffer shape, their mean form indices being 1.07 and 1.03, respectively. Grafts 1A, 1B, 1C, and 1D bear fruits showing wider ranges in form than do the fruits of grafts 2A and 2B, but many of them are typical Bartletts in form and their mean form indices are much closer to the 1.25 to 1.35 form index than they are to the 1.00 form index of Kieffer. These differences in shape can not be attributed to stock influence because all the scions were top worked on the one stock (Kieffer).

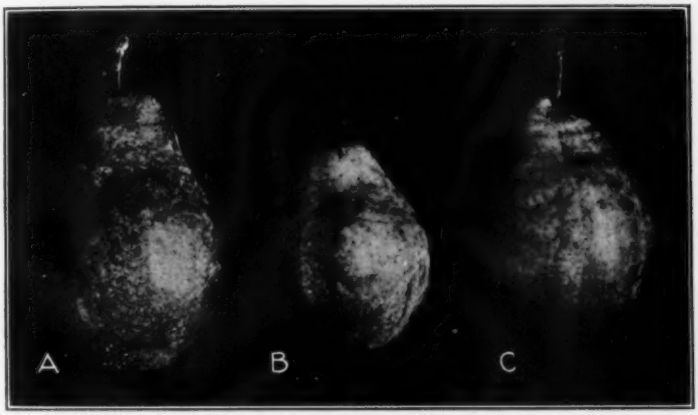

FIGURE 6.—Normal (A) and "Keiffer-shaped" (B and C) specimens of the striped Bartlett. These particular fruits show only indistinct stripes because of their advanced degree of maturity

TABLE 3.—*Frequency distribution of the form indices of fruits borne by different striped Bartlett grafts*

[Form index determined by dividing the axial diameter of the fruit by its transverse diameter, both having been measured to the nearest eighth of an inch]

Form-index class	Number of pears in class borne by tree or branch indicated										
	1-A	1-A-1	1-A-2	1-A-3	1-A-4	1-A-5	1-B	1-C	1-D	2-A	2-B
0.93 to 0.97									3	7	8
0.98 to 1.02	4	1		1	2				13	19	44
1.03 to 1.07	15	5		2	8		1	1	57	42	42
1.08 to 1.12	20	10		1	8	1	2	3	49	29	22
1.13 to 1.17	20	16			4		18	9	92	17	3
1.18 to 1.22	6	4			1	1	13	9	90	6	1
1.23 to 1.27	12	7	1		4		22	7	50		
1.28 to 1.32	3	2			1		5	6	11		
1.33 to 1.37	3	1	1		1		7	3	4		
1.38 to 1.42							3		1		
1.43 to 1.47							1				
1.48 to 1.52											
1.53 to 1.56								1			
Total	83						72	39	370	120	123
Weighted average of form indices	1.15						1.24	1.23	1.15	1.07	1.04

Before harvesting it was noticed that the fruits borne by graft 1A not only seemed somewhat less typically Bartlett in form than those of grafts 1B, 1C, and 1D, but also that several of the individual branches of this graft differed rather markedly from each other. Consequently they were harvested separately. The form indices of the fruits borne by these different lateral branches appear in separate columns in Table 3. Obviously, the numbers are not great enough to warrant attaching much significance, and another year's or several years' records must be obtained and propagation tests resorted to before conclusions can be drawn. It may be pointed out, nevertheless, that the same tendency toward dimorphism or polymorphism, toward segregating out into fairly distinct shape types, is evident in the lateral branches of graft 1A as is evident when grafts 1A, 1B, 1C, and 1D are compared with grafts 2A and 2B.

It is recognized that the forms that are here called form segregates are probably incomplete segregates, just like the first color selections. Especially is this true of the so-called normal Bartlett form that is found to some extent in grafts 1A, 1B, 1C, and 1D.

Field and laboratory studies now in progress indicate that many normal Bartlett trees, that is, those producing the normal green fruits, now growing in commercial orchards present this same diversity in fruit shape and that more or less segregation of the type here described is taking place.

No correlation was found between degree or amount of color striping and segregation as to form, some of the predominantly yellow fruits being Kieffer shaped, others typically Bartlett shaped. Similarly, some of the fruits that were predominantly green were Kieffer shaped, while others were of the normal Bartlett form. The evidence, therefore, indicates that out of the one parent limb sport at least four strains have been segregated—two in color and two in shape. The color segregates were the result of artificial selection; the form segregates were purely accidental.

DISCUSSION

Though the data here recorded pertain to a type of variation that in itself is of little importance in fruits, they throw light on what seems to be a fundamental, though little recognized, characteristic of many bud variations in fruits. This particular variation obviously did not appear as a departure from type at once permanent and fixed, ready to propagate true indefinitely as a uniform new strain or variety (uniform in the sense of meeting the usual specifications of a vegetatively propagated variety). It was a new strain, but a variable, segregating strain from which several fairly definite concrete forms could be developed. This was possible only by what has generally been termed bud selection, and furthermore the evidence indicates that these forms, once developed, can be maintained as clear-cut entities only by a continuation of the same process. This is not surprising in view of what has come to be common practice among experienced propagators of certain ornamental plants such as *Pandanus veitchi*. Incidentally the facts presented raise the question as to whether or not, if more or less continuous selection is necessary in maintaining the identity of certain bud sports, is it not likewise necessary in maintaining the identity of some of the parent varieties from which they may be derived?

SUMMARY

There is described a sectorial chimera of the Bartlett pear from which has been segregated two color forms and two forms differing from each other in shape of fruit.

The bark of the young shoots of the predominantly yellow segregate contains much less and its leaves contain somewhat less chlorophyll than corresponding tissues of the predominantly green segregate or of the parent all-green form.

Segregation as to color of bark and skin of fruit is independent of segregation as to shape of fruit.

The evidence indicates that continued selection is necessary properly to maintain, as well as to isolate, the types resulting from segregation.

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